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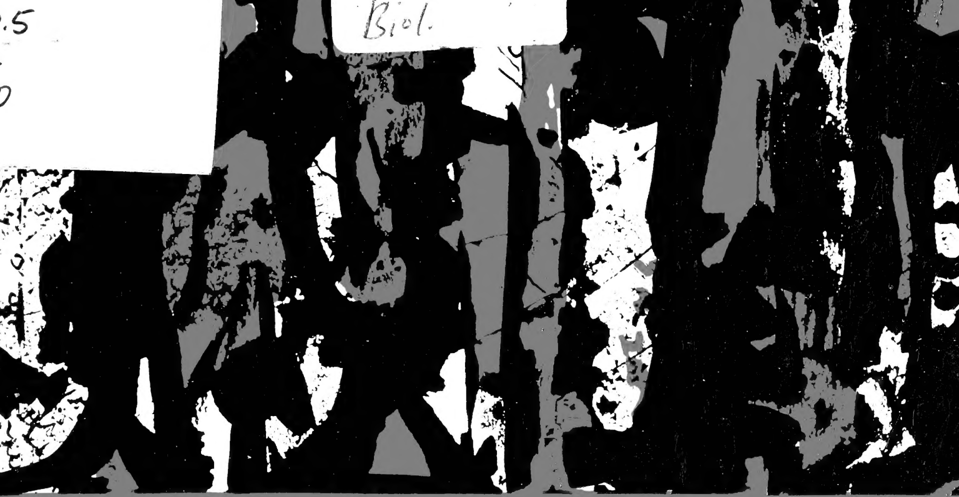

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Invertebrate Populations of the Deciduous Forest: Fluctuations and Relations to Weather

S. CHARLES KENDEIGH

ILLINOIS BIOLOGICAL MONOGRAPHS 50

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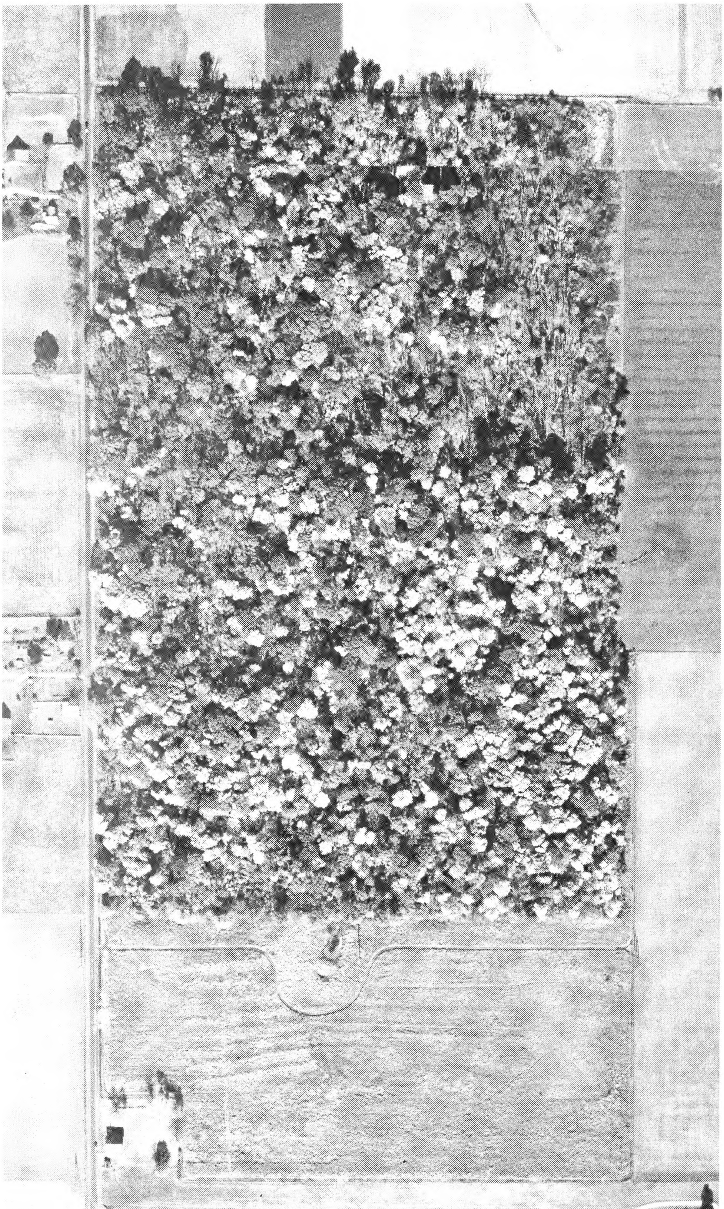

Invertebrate Populations of the Deciduous Forest: Fluctuations and Relations to Weather

S. CHARLES KENDEIGH

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Frontispiece: Aerial photograph of William Trelease Woods taken on October 28, 1958. Light-colored trees are mostly sugar maples, dark-colored ones red oak and other species. Standing dead elm trees are especially noticeable in the upper right-hand corner. *University of Illinois Air Photo Repository (UI-1-10 and 12).*

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1. Introduction

Animal populations are well known to fluctuate in size seasonally as the result of reproduction and mortality and annually because of changes in weather, predator-prey relations, diseases, food supply, and other factors. Quantitative measurements of fluctuations in invertebrate populations have seldom, however, been taken over long periods of time, except for some pest species, because such measurements are laborious, time-consuming, and, at best, only approximations. Quantification of variations in population size under natural conditions over months or years should facilitate the determination of the cause of fluctuations.

The major objectives of the present study are to analyze (a) the composition and relative population sizes of the larger invertebrate fauna of relatively undisturbed, near-virgin, stands of deciduous forest, (b) how the population size of each taxon fluctuates throughout the year, (c) how populations vary from year to year, and (d) how these fluctuations correlate with weather conditions. An attempt is made to show the relative importance of different weather variables and to provide equations for predicting population size when prevailing weather conditions are known.

The relation of insect populations to weather has long been of interest; the comprehensive treatments by Uvarov (1931) and Andrewartha and Birch (1954) are noteworthy. These authors believe weather conditions or climatic factors are more important in determining population levels than are predation, parasitism, or other density-dependent factors. Uvarov pointed out the difficulty, however, of predicting insect outbreaks, even after correlations with weather conditions are established, because weather cannot be forecast far in advance with much confidence.

Elton's publication (1966) is a long-term, intensive study, begun in 1945, of a deciduous forest stand — Wytham Woods — in England, but he was primarily concerned with dynamic relations between

populations as they formed a community pattern. He credits V. E. Shelford's "Animal communities in temperate America" (1913) for "the first systematic attempt to codify terrestrial communities." For this publication Shelford counted very few animals; however, he was aware of the importance of animal numbers. Soon after the University of Illinois acquired William Trelease Woods, he and his graduate students began to measure invertebrate populations in order to see how they varied with the time of day and season, from year to year, between strata, and in successional communities (Weese, 1924; Blake, 1926, 1931; Smith, 1928; Davidson, 1930, 1932; Carpenter, 1935). In 1933 Shelford initiated a long-term quantitative study of both seasonal and annual populations in the William Trelease Woods, which was continued with the help of graduate student assistants until he retired from teaching in 1946. At that time I took over the project and maintained it until 1971, when I also approached retirement. Meanwhile, incorporation of Brownfield Woods and Funk Forest into the sampling program increased the breadth of the study.

Shelford (1951a, b) undertook a graphical analysis of the first 14 years' data to seek correlations between fluctuations in yearly populations and weather conditions for some 50 species of invertebrates. He found temperature not to be important but rainfall and ultraviolet radiation to be very significant, especially their interrelations during a sensitive period usually near the beginning of the reproductive phase of the life cycle. The present study covers the data obtained over a 38-year period, including the early years considered by Shelford. These more extensive data permit statistical treatment with the use of multiple regression procedures.

2. Location of Raw Data

The records showing taxa and number of invertebrate animals collected on each date in each of the three woods, monthly summaries of population data for each taxon, microclimatic data, and phenology of plant species for individual years are filed in the archives of the University of Illinois Main Library at Urbana, Illinois. Filed here also is a chronological list of the persons responsible for making and recording the collections and the period(s) during which they served. These records are available for use by other investigators.

3. Location and Description of the Study Areas

The three areas studied lie in the former ecotone between prairie and deciduous forest (Fig. 1) or in the prairie peninsula section of the oak-hickory forest region described by Braun (1950). They are likewise in the till plains of the central lowlands physiographic division. The till was deposited during the Wisconsin glaciation and is overlaid by loess.

The study was centered in the William Trelease Woods, approximately 6.4 km (4 miles) northeast of Urbana, Champaign County, in east-central Illinois (40° 08′N, 88° 18′W). The first systematic collecting was begun here in mid-1933. Brownfield Woods lies 2.4 km (1.5 miles) northwest of William Trelease Woods and about 4.8 km (3 miles) from Urbana; collections were begun here in 1949. Both areas were part of the so-called Big Grove, a prairie grove once covering about 26 km^2 (10 square miles) along the West (Saline) Branch of the Salt Fork River (Fig. 2). Before the advent of white settlers, this grove was surrounded by tallgrass prairie. At present, the two woods

Fig. 1. Location of Champaign-Urbana in the ecotone between deciduous forest (stippled) and tallgrass prairie (plain) (modified from Shelford, 1963).

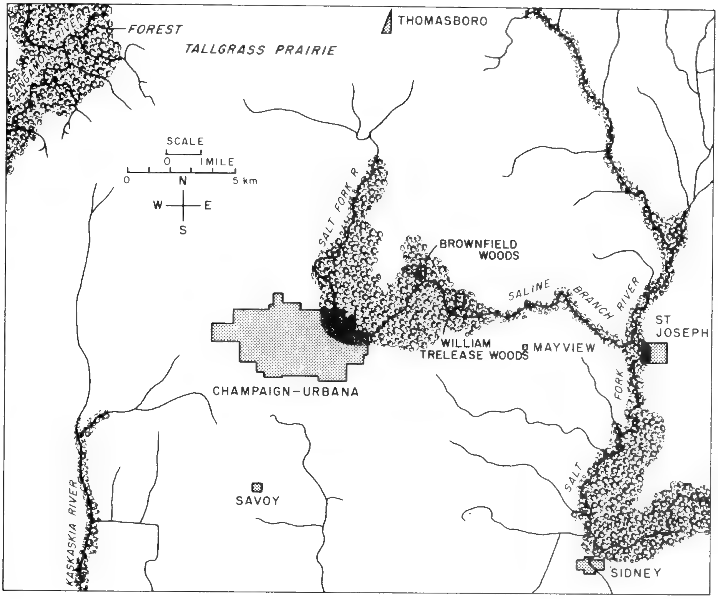

Fig. 2. Location of William Trelease and Brownfield Woods in relation to Champaign-Urbana and primitive vegetation.

are surrounded by farmlands and are no longer connected by continuous forest. Both woods are rectangular in shape and each contains about 24 ha (60 acres). Funk Forest lies in McLean County, a little over 80 km (50 miles) west-northwest of Urbana. It also contains approximately 24 ha (60 acres) but is continuous on its north boundary with a much larger tract of mature forest, the remnant of a prairie grove along Timber Creek that originally covered 10 to 13 km^2 (4-5 square miles). Collecting was started here in 1955. Collecting in all three areas terminated in 1971, so that the number of years entering into this analysis is for William Trelease Woods, 38; Brownfield Woods, 23; and Funk Forest, 17.

William Trelease Woods

William Trelease Woods was acquired by the University of Illinois in 1917-18 and has been protected from undue disturbance since then. Previously the woods was grazed, and the southern half served as a woodlot. There is the remnant of an old well near the south boundary. Some *Juglans nigra* Linnaeus (black walnut) was removed in

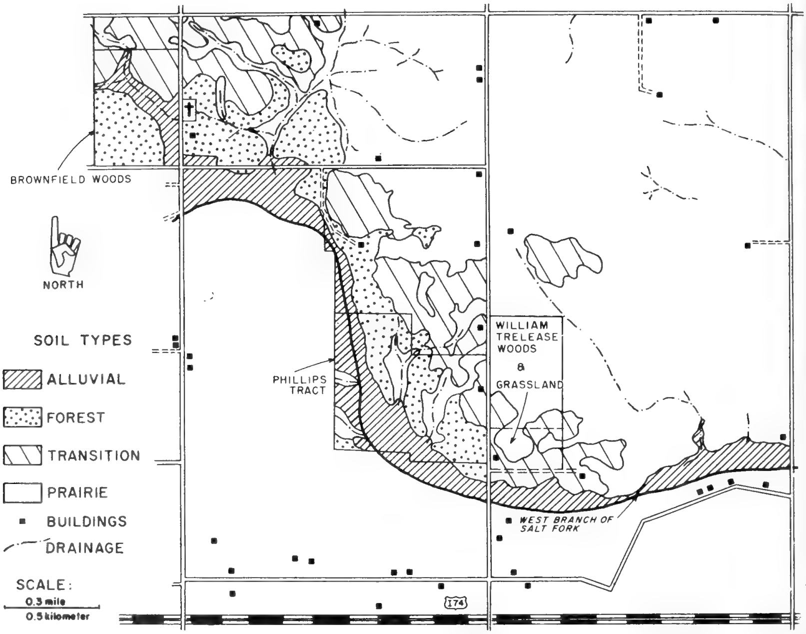

Fig. 3. Location of William Trelease and Brownfield Woods in relation to surrounding farmlands, soil types, and drainage.

the early days, but the area quickly recovered. When this study was initiated after one and a half decades of protection, it had many characteristics of a virgin forest. In 1936 a small pond was excavated about midway inside the east boundary, and in 1943 another small pond was made just outside and midway along the south boundary. The area is surrounded on the west by a country road and two farm homes, on the north and east by farmland, and on the south by a restored prairie which was started in 1943. There is very little topographic relief, and the soil in the early spring remains saturated with water for days at a time. This is the wettest of the three woods studied. Brunizem-like soils are most prevalent with transitional types to gray-brown podzolic soils. The woods has developed on upland soils that were covered with tallgrass prairie 400 to 600 years ago (Fig. 3).

The present stand is composed of 368 trees (7.6 cm and above in diameter at breast height) with a basal area of 21 m^2ha^{-1}. Thirty-seven woody species occur; the principal ones in descending order of importance are presently *Acer saccharum* Linnaeus (sugar maple), *Celtis occidentalis* Linneaus (hackberry), *Fraxinus americana* Linnaeus

(white ash), *Ulmus rubra* Mühlenberg (slippery elm), *Tilia americana* Linnaeus (basswood), *Quercus rubra* Linnaeus (red oak), and *Aesculus glabra* Willdenow (Ohio buckeye). Before the early 1950s *Ulmus americana* Linnaeus (American elm) was a predominant species, but phloem necrosis and Dutch elm disease have since decreased it to minor importance. There are some very large *Quercus macrocarpa* Michaux (bur oak), *Q. muehlenbergii* Engelmann (chinquapin oak), and red oak scattered through the area. Sugar maple formerly covered about 30 per cent of the woods, mixed hardwood 45 per cent, and elm 25 per cent. From the 1950s into the 1960s with the decrease in American elm, there has been an increase in slippery elm and hackberry. Sugar maple has remained about the same (Boggess, 1964). The relatively dense understory is predominantly *Asimina triloba* (Linnaeus) Dunal (pawpaw) and *Lindera benzoin* (Linnaeus) Blume (spice-bush). There is a rich flora of herbaceous plants in the spring (Jones, 1947), while in summer *Laportea canadensis* (Linnaeus) Gaudichaud-Beaupré (wood nettle) is ubiquitous. Most of the population sampling was around stake N2W2, 50-150 m inside the west border, and 100 m north of the center.

Brownfield Woods

During the early part of the century Brownfield Woods was heavily used by the public for picnics and family outings, and some trees, particularly walnuts, were removed. The University of Illinois obtained a lease of the area in the 1920s and purchased it in 1939, so that it has been fully protected for 50 years. It has never been clear cut, and some of the bigger trees are more than 375 years old. General topography is that of a rolling upland. The most conspicuous topographic feature is the shallow valley of a small intermittent stream that extends diagonally across the area from the northwest to the southeast. Maximum relief is about 9 m. Two soil groups are the gray-brown podzolic and brunizem-like soils with transitions between the two. All collections were made near the middle of the woods on the north side of the stream on transition-type soils. The mixed mesophytic forest contains 279 trees with a basal area of 26 m^2ha^{-1}. Twenty-five species of trees and shrubs are present, with sugar maple and red oak the principal dominants. Seedlings of sugar maple are abundant in the undergrowth. The American elm has greatly decreased since the occurrence of phloem necrosis and Dutch elm disease in the 1950s (Boggess and Bailey, 1964).

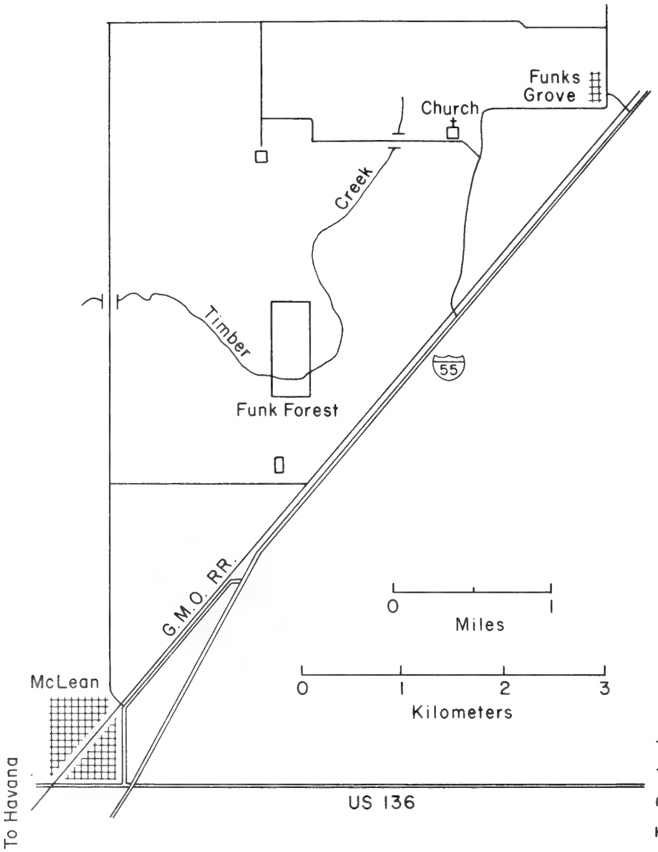

Fig. 4. Location of Funk Forest (after Calef, 1953).

Funk Forest

Funk Forest is a relatively undisturbed remnant of the original forest (Calef, 1953) and was acquired by the University of Illinois in 1950. Some grazing occurred previously. Timber Creek crosses the area about a quarter of the distance from the south end (Fig. 4). The south creek bank rises sharply and forms a bluff up to 12 m high. Most of the collecting was done on the upland between the bluff and the south boundary. This area is cut by 4 deep gullies that drain into the creek, and it contains well-developed gray-brown podzolic forest type soil. The forest as a whole consists of 333 trees with a basal area of

27 m^{2}ha^{-1} and includes 40 woody species. Sugar maple is the leading dominant, followed closely by *Quercus alba* Linnaeus (white oak) and slippery elm. White oak does not occur prominently in either William Trelease or Brownfield Woods and probably represents a pioneer species here that is on the way out. Sugar maple is on the increase, as evidenced by the large number of seedlings and young trees. The American elm has suffered from the elm diseases in the last two decades. Funk Forest is somewhat more similar to Brownfield than it is to William Trelease Woods (Boggess and Geis, 1966).

Phenology of Conspicuous Plant Species

During the winter there may be a few dry leaves clinging to some trees, but the trees are otherwise bare. The ground is more or less covered with decaying leaves, and there are some standing dead grasses. A few herbs close to the ground remain green overwinter. Early spring is conspicuous with a rich ground cover of flowers. The first new green leaves begin to appear above ground during the second week in March and the first flowers, usually *Claytonia virginica* Linnaeus (spring beauty), a couple of weeks later (Table 1). With the closing of the tree canopy, these flowers disappear and in summer are replaced by abundant wood nettle. The buds of elm and Ohio buckeye begin to open during the second or third week of March followed by sugar maple and red oak in early April, but tree foliage does not develop much before the third week in April and is not fully developed until mid- to late May. The tree foliage begins to acquire its autumn coloration in late September, and the leaves have mostly fallen by early November, although they persist longer on the oaks.

Table 1. Phenology of conspicuous plants: median dates for the period 1949 through 1964, as observed by Charles W. Smith in William Trelease and Brownfield Woods

	Leaf Buds Opening	First Flowering	Leaves Dropped
TREES			
Ulmus spp. (elm)	Mar. 14	———	Nov. 10
Aesculus glabra Willdenow (Ohio buckeye)	Mar. 24	Apr. 25	Oct. 13
Acer saccharum Marsh (sugar maple)	Apr. 6	———	Nov. 10
Crataegus spp. (hawthorn)	Apr. 7	Apr. 29	Nov. 1
Quercus rubra Linnaeus (red oak)	Apr. 11	———	Nov. 18+

Table 1 (Continued)

SHRUBS, VINES			
Rosa setigera Michaux (climbing rose)	Apr. 4	May 20	Oct. 20
Asimina trilobata (Linnaeus) Dunal (pawpaw)	Apr. 9	Apr. 28	Nov. 10
Lindera benzoin (Linnaeus) Blume (spice-bush)	Apr. 18	Apr. 7	Oct. 22
HERBS			
Claytonia virginica Linnaeus (spring beauty)	Mar. 11	Mar. 24	———
Viola spp. (violet)	Mar. 28	Apr. 17	———
Trillium recurvatum Beck (purple trillium)	Mar. 28	Apr. 19	———
Sanguinaria canadensis Linnaeus (bloodroot)	Mar. 30	Apr. 5	———
Mertensia virginica (Linnaeus) Link (bluebell)	Mar. 30	Apr. 20	———
Hepatica acutiloba DeCandolle (hepatica)	Apr. 2	Apr. 26	———
Erythronium albidum Nuttall (white trout-lily)	Apr. 8	Apr. 17	———
Podophyllum peltatum Linnaeus (May-apple)	Apr. 10	May 3	———
Laportea canadensis (Linnaeus) Gaudichaud-Beaupré (wood nettle)	Apr. 20	July 12	———

4. The Climatic Environment

Macroclimate

Macroclimate temperatures, as taken in Fahrenheit at the U.S. Weather Bureau station in Urbana, normally reach a minimum in January and a maximum in July with a range between mean monthly extremes of 48.4°F (26.9°C) (Fig. 5). Monthly mean minimum temperatures reach a low of 18.9°F (−7.3°C) in January and mean maximum temperatures a high of 86.3°F (30.2°C) in July.

Normal precipitation is 2 inches or more (5 cm) every month of the year, with minimum amounts during the winter, often as snow, and maximum amounts in May and June. Snowfall averages about 21 inches (53 cm) per year.

The photoperiod at mid-month varies from 15.0 hours of daylight in June to 9.35 hours in December. There is a range of ultraviolet intensity of 36.6 gcal cm^{-2} day^{-1} from a minimum in December to a maximum in July.

The locality, therefore, has considerable seasonal variation in weather to which animal populations may be expected to respond.

Microclimate

A hygrothermograph was run in a standard Weather Bureau shelter placed about 1.5 m above the ground in an exposed location in tallgrass prairie immediately south and adjacent to William Trelease Woods. Monthly mean temperatures were calculated from bi-hourly readings during 1950 and 1951 and compared with monthly means from the Weather Bureau station in Urbana about 9.7 km (6 miles) away. Weather Bureau means are based on averages of daily maximum and minimum temperatures. In 17 of the 24 comparisons, Trelease Grassland temperatures were lower than the Weather Bureau temperatures. The mean difference (± SD) for all 24 months was −0.26° ±0.68°F (−0.14° ± 0.38°C).

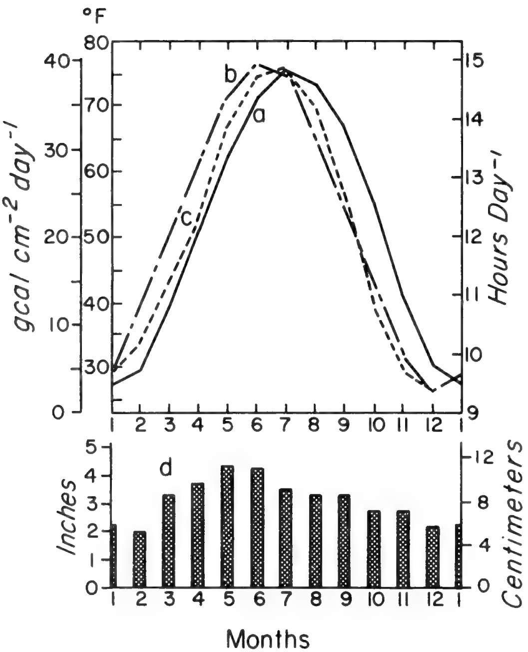

Fig. 5. Yearly cycle of (a) normal mean monthly temperature (°F), (b) photoperiod (hours day^{-1}), (c) ultraviolet radiation (gcal cm^{-2} day^{-1}), and (d) normal precipitation (inches, cm).

Another hygrothermograph was run in a similar shelter but well inside William Trelease Woods, and comparisons were made with the adjacent Trelease Grassland temperatures for 28 months between August, 1949, through the end of 1951 (the record for December, 1949, is incomplete and omitted). Temperatures inside the woods were equal to or higher than the grassland temperatures during January, February, and March, but tended to be lower during the rest of the year. However, there were several fluctuations of monthly temperatures in the woods above those in the grassland during this latter period, so that the differences between the two periods are not statistically significant. The mean difference for all months is $-0.61° \pm 2.20°F$ ($-0.34° \pm 1.22°C$). This makes the mean difference between the woods and Weather Bureau temperatures, $-0.87°F$ ($-0.48°C$), very similar to that recorded for another forested area west of Urbana (Johnson et al., 1975). For our purpose, the difference is not significant.

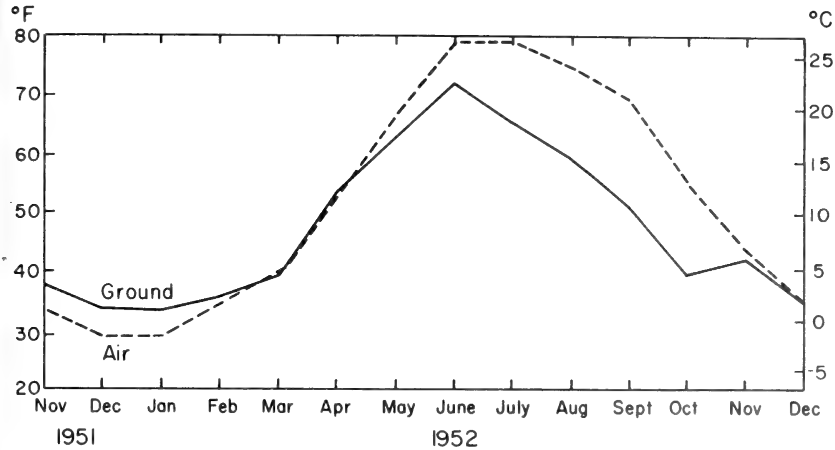

Fig. 6. Yearly cycle of ground and air temperatures in William Trelease Woods.

From November, 1951, through December, 1952, a soil thermograph recorded ground temperatures inside William Trelease Woods at a depth of 6.35 cm (Fig. 6). Monthly means were obtained by averaging daily maximum and minimum temperatures for both the below-ground and the woods thermographs, the latter at about 150 cm above the ground. During the winter months ground temperatures averaged higher than air temperatures, which is favorable for the many species that overwinter in the ground. During the spring, as temperatures rose, air and ground temperatures were about the same. From May through October ground temperatures averaged well below air temperatures. Weese (1924) found that ground temperatures about 10 cm below the surface and air temperatures 60 cm above the surface in William Trelease Woods varied in the same manner as shown here, but differences between the two levels were appreciably less. Daily fluctuations in temperature are nearly always less below ground than they are above ground.

Standard Weather Bureau rain gauges were placed in the Trelease Grassland tract in an exposed situation south of the woods, at two locations well inside William Trelease Woods, and at one location near the center of Brownfield Woods. Measurements of precipitation extended over 22 years, between 1949 and 1971 (1963 missing). The Trelease Grassland's gauge averaged 1.54 ± 1.27 inches (3.91 ± 3.23 cm) per year or 4.2 per cent lower than the Weather Bureau

station in Urbana. During only 3 years did the grassland's gauge collect more precipitation than the Urbana gauge. Snowfall is included in these figures as water.

The two gauges inside William Trelease Woods averaged 3.75 ± 1.96 inches (9.52 ± 4.98 cm) precipitation per year, or 10.6 per cent less than in the exposed grassland gauge; the gauge in Brownfield Woods averaged 2.24 ± 1.54 inches (5.69 ± 3.91 cm) per year, or 6.4 per cent less. Stem-flow down the tree trunks, interception by the tree canopy, and evaporation back into the air probably accounted for the difference. A month-by-month comparison of the measured precipitation in the two woods and the grassland showed no consistent difference between winter when the trees were bare and summer when they were in full foliage. Effective precipitation that reaches the ground in these two woods is thus 4-5 inches (10-13 cm) less than that recorded by the Urbana Weather Bureau station, except for what reaches the ground from the stem-flow down the tree trunks, which was not measured.

Although not measured in William Trelease or Brownfield Woods, the incident total solar radiation at ground level is probably maximum for the year in April and minimum from September through January. With open exposure, radiation reaches a maximum in July, but the canopy foliage of the trees and shrubs intercepts most of it during the summer months (Johnson et al., 1975).

In assessing the importance of the various weather parameters as they affect fluctuations in the population, as discussed later, it is well to keep in mind these relations between the macroclimate and the microclimate to which the animals are actually exposed.

Critical Weather Factors

Shelford (1951a) pointed out that determination of the sensitive or critical period in the yearly cycle of a species' activities is of great importance in correlating population and weather fluctuations. The critical period covers the few days or weeks when the species is most sensitive to weather conditions. This period may come when they are mating and egg-laying, while the eggs are hatching, during larval or pupal stage, or during winter dormancy. Weather may have minimal influence on mortality or natality except during the critical period and, unless the critical period can be discovered, attempted correlations of population size with weather conditions may be unrewarding. Since our population data are averaged on a monthly basis, for rea-

sons described later (p. 25), this is the shortest feasible period for consideration of weather factors.

By using mean monthly temperatures separately during May, June, and July, location of the critical period for reproduction during the year being analyzed is sought. By using temperatures during these same months but during the previous year, an attempt is made to determine whether conditions affecting the success of reproduction one year carry over to the following year, whether similar weather conditions during two successive years have an accumulative effect, or whether dissimilar weather during two successive years counteract each other in any way. The relation between populations and a weather factor is not necessarily linear; it may be curvilinear. There are a number of curvilinear relationships possible, but correlations are attempted only with the square of mean monthly temperature. Finally, the average monthly mean minimum during the winter season is important for evaluating the effect of prevailing conditions on mortality during the dormancy period. Using the mean minimum, rather than the record low, for the winter period puts emphasis on the possible accumulative effect of prevailing cold instead of the action of extreme cold of very short duration, although conceivably both may be involved. Uvarov (1931) stated that the mortality of insects caused by winter cold is probably the main factor controlling the abundance of most insects in temperate latitudes.

Precipitation may have a more direct effect on mortality of eggs and immature stages than on the adults, but adults may also be affected. Likewise, precipitation may have an indirect effect by influencing the growth of plants on which the animals feed. The precipitation data are handled in a similar way as the temperature data.

There may well be synergistic action between weather factors in their influence on population size, as Shelford (1951a) has already shown. An attempt is made to determine if such interactions should be further pursued by considering the product of temperature and precipitation during certain months.

Snowfall may influence population size by the amount of insulation furnished dormant animals during the winter cold period.

Shelford (1951a, b) found significant correlations between fluctuations in population and ultraviolet solar radiation, particularly as the latter related to precipitation. Unfortunately, continuous recordings of ultraviolet wavelengths are not available. I have resorted to average monthly measurements of daily total radiation (gcal cm^{-2}) as determined by a pyrheliometer mounted on the roof of a building

on the University of Wisconsin campus at Madison approximately 370 km (230 miles) away. There was some possible smoke contamination from the university heating plant, nearby railroads, and suburban developments, and cloud cover no doubt varied from that over the study area. Values of total radiation are corrected to ultraviolet radiation by using monthly ratios of biologically effective ultraviolet (approximately 2900 Å to 3150 Å) to total solar and sky radiation (Table 2). Radiation intensity is calculated for the current year's reproductive season and for a longer period the preceding year. It is to be kept in mind that the data for seasonal and yearly fluctuations in ultraviolet intensity are based on a constant fraction of the measured total radiation, and that ultraviolet radiation may not fluctuate from year to year in the same manner or degree as does total solar radiation. Furthermore, solar radiation measurements have been generally deficient both in quality and quantity. The instrumentation does not record the shorter wavelengths adequately, and over the whole range it may commonly be in error by 5-10 per cent (Bennett, 1965). If considered only as a rough index, it has some value.

Altogether, the roles of 31 weather variables were analyzed as to their influence on the size of yearly populations. In addition, the population the previous year obviously influences the size of the population the following year and may modify correlations made with the weather factors (Table 3). Yearly fluctuations in some of the weather factors over the period of study are shown in Figs. 7-10.

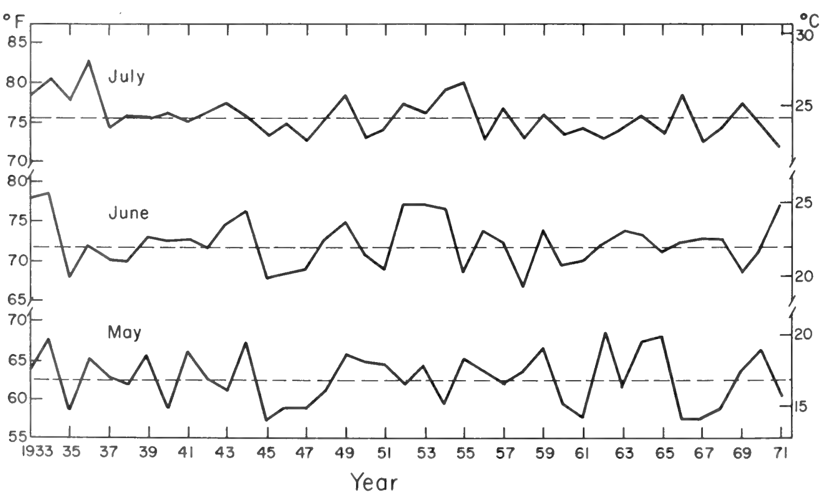

Fig. 7. Yearly fluctuations in mean monthly temperatures at the Urbana U.S. Weather Bureau station. Dashed lines indicate the mean for the period of study.

Table 2. Monthly ratios of biologically effective ultraviolet (approximately 2900 Å to 3150 Å) to total solar and sky radiation (Coblentz, 1952)

January	0.0241	July	0.0703
February	0.0297	August	0.0689
March	0.0408	September	0.0654
April	0.0519	C ctober	0.0479
May	0.0621	November	0.0307
June	0.0680	December	0.0202

Table 3. Key for identification and average values of weather variables for the period of study, 1934-1971 inclusive, from the Urbana station of the U.S. Weather Bureau

Variable	Symbol	Mean ± SD	Variable	Symbol	Mean ± Sd
		TEMPERATURE (°F)			
May	T_1	62.5 ± 3.5	May, previous year	T_7	62.5 ± 3.6
June	T_2	71.8 ± 2.8	June, previous year	T_8	72.0 ± 3.0
July	T_3	75.6 ± 2.4	July, previous year	T_9	75.8 ± 2.5
May, squared	T_4	3915 ± 441	May, previous year, squared	T_{10}	3920 ± 448
June, squared	T_5	5168 ± 402	June, previous year, squared	T_{11}	5199 ± 434
July, squared	T_6	5720 ± 367	July, previous year, squared	T_{12}	5746 ± 390
			Mean minimum, prev. Dec.-Feb.	T_{13}	21.4 ± 3.1
		PRECIPITATION (in.)			
Apr., May	P_1	8.2 ± 2.5	Apr., May, prev. yr.	P_6	8.0 ± 2.7
June, July	P_2	8.1 ± 2.8	June, July, prev. yr.	P_7	8.1 ± 2.8
Aug., Sept., Oct.	P_3	8.9 ± 3.3	Aug., Sept., Oct., previous year	P_8	8.9 ± 3.3
Total yearly	P_4	37.3 ± 5.2	Total, prev. yr.	P_9	37.3 ± 5.2
Total yearly, squared	P_5	1419 ± 379	Apr., May, squared	P_{10}	73.0 ± 46.5
			June, July, squared	P_{11}	73.3 ± 46.6
		PRECIPITATION (in.) × TEMPERATURE (°F)			
May	TP_1	256 ± 132	July	TP_3	279 ± 140
June	TP_2	313 ± 147			
		SNOW (in.)			
Dec., Jan., Feb.	S_1	15.0 ± 7.7	Dec., Jan., Feb. squared	S_2	281 ± 283
		ULTRAVIOLET (gcal cm^{-2}day^{-1})			
Apr.-July	U_1	32.2 ±1.6	Apr.-Oct., prev. yr.	U_2	28.3 ± 1.3
		POPULATION (individuals m^{-2})			
Previous year	PP				

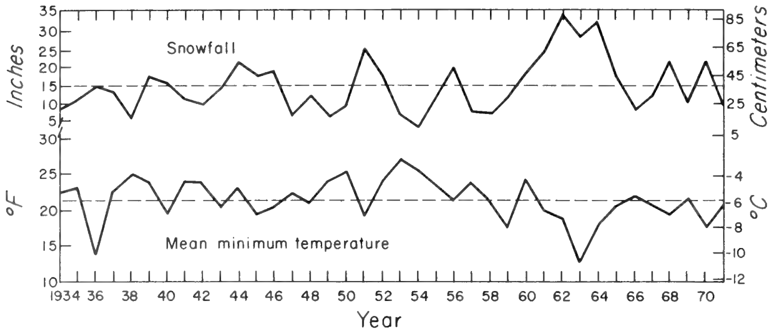

Fig. 8. Yearly fluctuations in snowfall and mean minimum temperature (December-February).

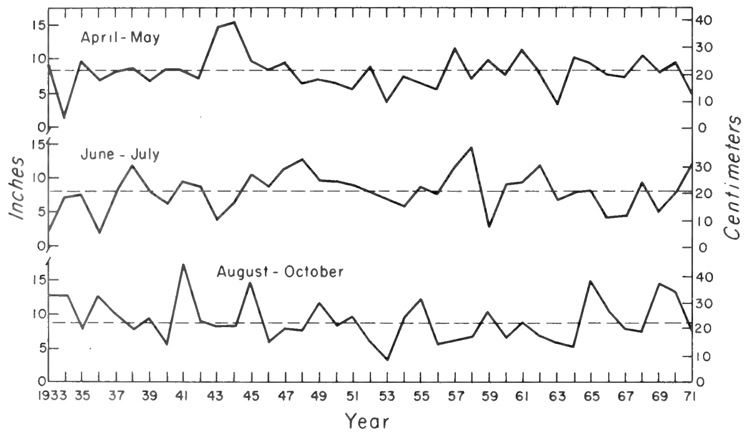

Fig. 9. Yearly fluctuations in precipitation.

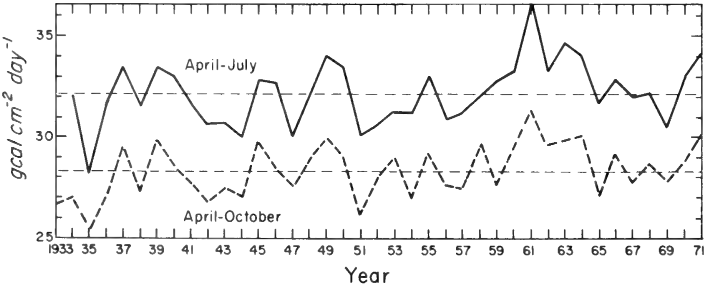

Fig. 10. Yearly fluctuations in ultraviolet intensity.

The U.S. Weather Bureau records temperature in degrees Fahrenheit and precipitation in inches, and the equations are in these units. Where measurements are taken in metric units, they need to be converted into English units for substitution in the equations.

Interrelations of Weather Variables

The weather variables are not completely orthogonal or independent of each other. The matrix of partial correlation coefficients in Table 4 shows the relation between any two variables while holding constant the values of the other variables.

Highest correlations (1.0) occur between a variable and that variable squared, as would be expected. The partial regression coefficients for these two variables usually, but not always, have opposite signs, and the coefficient for the squared variable is always smaller than for the unsquared variable.

June and July temperatures are negatively correlated with June and July precipitation (partial correlation coefficients, r, of about -0.4) for both the current and preceding years.

Precipitation during April and May, June and July, and August through October is correlated with total yearly precipitation, with partial correlation coefficients, r, of from $+0.3$ to $+0.5$ for the current and preceding years.

ble 4. Matrix of partial correlation coefficients for weather parameters

	T_1	T_2	T_3	T_4	T_5	T_6	T_7	T_8	T_9	T_{10}	T_{11}	T_{12}	T_{13}
	1.00												
	0.23	1.00											
	0.05	0.24	1.00										
	1.00	0.23	0.04	1.00									
	0.23	1.00	0.24	0.22	1.00								
	0.05	0.23	1.00	0.04	0.24	1.00							
	−0.18	0.00	−0.12	−0.18	0.00	−0.12	1.00						
	−0.14	−0.02	0.13	−0.13	−0.01	0.13	0.31	1.00					
	0.06	−0.10	0.03	0.06	−0.09	0.04	0.13	0.33	1.00				
10	−0.19	−0.01	−0.12	−0.19	0.00	−0.12	1.00	0.30	0.13	1.00			
11	−0.14	−0.02	0.14	−0.14	−0.01	0.13	0.31	1.00	0.33	0.30	1.00		
12	0.06	−0.10	0.03	0.06	−0.10	0.04	0.14	0.33	1.00	0.13	0.33	1.00	
13	0.03	0.19	0.05	0.03	0.19	0.05	0.05	0.42	0.40	0.04	0.42	0.39	1.00
	−0.06	0.06	0.04	−0.05	0.06	0.03	−0.12	0.00	−0.09	−0.13	0.00	−0.09	−0.07
	0.00	−0.40	−0.48	0.00	−0.39	−0.48	−0.06	0.05	−0.17	−0.07	0.05	−0.16	0.14
	0.24	−0.27	0.22	0.25	−0.28	0.22	−0.06	0.01	0.11	−0.06	0.01	0.10	0.02
	0.13	−0.34	−0.09	0.14	−0.34	−0.09	−0.11	0.03	−0.16	−0.11	0.03	−0.16	0.13

Table 4 (Continued)

	T_1	T_2	T_3	T_4	T_5	T_6	T_7	T_8	T_9	T_{10}	T_{11}	T_{12}	T
P_5	0.13	−0.32	−0.10	0.13	−0.32	−0.10	−0.08	0.06	−0.16	−0.08	0.06	−0.16	05
P_6	0.16	−0.19	−0.25	0.16	−0.19	−0.24	−0.16	−0.10	−0.10	−0.16	−0.10	−0.11	−06
P_7	0.16	0.05	0.06	0.15	0.05	0.06	−0.01	−0.38	−0.46	−0.01	−0.38	−0.46	−04
P_8	−0.21	−0.23	−0.02	−0.21	−0.24	−0.02	0.25	−0.17	0.29	0.26	−0.17	0.30	04
P_9	−0.03	−0.24	−0.19	−0.03	−0.24	−0.19	0.12	−0.34	−0.11	0.12	−0.35	−0.11	−05
P_{10}	−0.03	0.15	0.04	−0.02	0.15	0.03	−0.09	0.04	−0.07	−0.10	0.04	−0.07	−04
P_{11}	0.12	−0.42	−0.42	0.01	−0.41	−0.42	−0.13	−0.03	−0.19	−0.14	−0.03	−0.19	05
TP_1	−0.17	0.09	0.05	−0.16	0.10	0.05	−0.23	−0.11	−0.09	−0.23	−0.11	−0.09	0.7
TP_2	−0.32	−0.29	−0.36	−0.32	−0.28	−0.37	−0.05	−0.02	−0.27	−0.06	−0.03	−0.27	0.
TP_3	0.37	−0.18	−0.23	0.37	−0.18	−0.23	−0.05	0.12	0.04	−0.05	0.12	0.04	0.4
S_1	0.27	0.04	−0.36	0.28	0.03	−0.36	−0.04	−0.24	−0.24	−0.03	−0.24	−0.23	−0.
S_2	0.31	0.07	−0.33	0.33	0.06	−0.33	−0.07	−0.18	−0.28	−0.06	−0.18	−0.27	−0.
U_1	0.07	0.01	−0.16	0.07	0.00	−0.16	−0.02	−0.16	−0.18	−0.02	−0.17	−0.17	−0.
U_2	0.21	0.00	−0.50	0.22	0.00	−0.50	−0.04	−0.08	−0.28	−0.04	−0.09	−0.28	−0.

	P_1	P_2	P_3	P_4	P_5	P_6	P_7	P_8	P_9	P_{10}	P_{11}
P_1	1.00										
P_2	−0.07	1.00									
P_3	0.08	0.14	1.00								
P_4	0.38	0.43	0.54	1.00							
P_5	0.34	0.44	0.54	1.00	1.00						
P_6	0.07	0.16	0.27	0.29	0.30	1.00					
P_7	−0.27	0.05	−0.09	0.02	0.03	−0.05	1.00				
P_8	−0.08	−0.09	−0.07	0.00	−0.02	−0.03	−0.15	1.00			
P_9	−0.17	0.02	−0.01	0.14	0.13	0.38	0.43	0.53	1.00		
P_{10}	0.98	−0.12	0.01	0.29	0.26	0.11	−0.25	−0.11	−0.16	1.00	
P_{11}	−0.07	0.97	−0.13	0.42	0.43	0.22	0.13	−0.14	0.05	−0.11	1.00
TP_1	0.69	−0.05	−0.06	0.23	0.21	0.17	0.00	0.01	0.15	0.70	0.01
TP_2	0.13	0.73	−0.13	0.37	0.36	0.03	−0.06	−0.15	−0.04	0.06	0.68
TP_3	−0.25	0.66	−0.07	0.23	0.25	0.16	0.14	0.02	0.04	−0.23	0.66
S_1	0.11	0.00	−0.17	−0.10	−0.11	0.11	−0.08	0.01	0.07	0.14	−0.07
S_2	0.07	0.07	−0.23	−0.12	−0.12	0.05	−0.04	−0.07	0.01	0.09	0.01
U_1	−0.17	0.06	−0.01	0.07	0.08	0.07	0.11	−0.07	0.02	−0.18	0.04
U_2	−0.13	0.16	−0.16	−0.01	0.01	−0.10	0.26	−0.17	0.03	−0.16	0.11

	TP_1	TP_2	TP_3	S_1	S_2	U_1	U_2
TP_1	1.00						
TP_2	−0.02	1.00					
TP_3	−0.06	−0.03	1.00				
S_1	−0.03	−0.07	0.06	1.00			
S_2	−0.08	−0.08	0.17	0.97	1.00		
U_1	−0.28	0.11	−0.03	0.35	0.36	1.00	
U_2	−0.12	−0.08	0.30	0.30	0.40	0.30	1.00

Both monthly temperatures and precipitation taken separately are correlated with their monthly products ($TP_{1,2,3}$), but the correlation of temperature is at a lower level ($r = -0.2$ to -0.3) than for precipitation ($r = +0.7$). Of a total of 745 significant partial regression coefficients that enter into the equations given later, only 53, or 7 per cent, deal with the TP variables.

Snowfall and mean minimum temperatures during the winter are negatively related ($r = -0.4$).

Ultraviolet radiation, April-October, shows a negative correlation with July temperatures ($r = -0.5$).

There are other scattered correlations in Table 4 that reach r values of 0.3 and 0.4. Very low correlations, for instance, occur between a weather factor one year and the factor for the same period the preceding year.

The partial correlation coefficients for the previous year's populations (PP) are not included in Table 4, as they vary with each taxon. One would expect, however, that PP would show correlations with the weather variables of the preceding year if, indeed, weather affects population size.

5. Methods of Censusing

General Comments

Only the more prominent and conspicuous species were censused. No attempt was made routinely to collect and count the smaller forms and those occurring in the tree stratum, in and under fallen logs, and deep in the soil. Irregular, scarce, or not easily identifiable species are included only in the totals for the genus, family, or order.

Counts were made of adults, juveniles, nymphs, and larvae, and the term "population," as used, applies only to these forms and excludes eggs and pupae. Adults, juveniles, and nymphs were not distinguished in the counts except in those taxa indicated, but larvae were censused separately.

The accurate measurement of invertebrate populations is very difficult, as is well known. Individuals are small, motile, secretive, sometimes colonial, sometimes nocturnal, and occupy a variety of small niches — to mention a few of the difficulties. An attempt was made to estimate number of individuals per square meter, but this is not stressed, and the numerical figures used should be considered primarily as indices of population size. Censusing was conducted separately for ground, herb, and shrub strata. The manner in which species are segregated into different strata at Trelease and Brownfield Woods has been shown by Weese (1924), Blake (1926), and Davidson (1930).

The censusing work was done by graduate student research assistants with the help of the Woods Custodians. The two Woods Custodians were not biologists but were trained to take sample collections in a uniform manner. It was hoped that their continuity with the program over many years would compensate, in part, for variations in the collecting effectiveness of the student assistants, who served for only short periods. They proved to be less efficient with the use of the sweep net for the herb and shrub collections, but their ground sampling appeared satisfactory.

Procedures

The Woods Custodian took all the *ground samples* on or near the same date each month on the following schedule:

William Trelease and Brownfield Woods: single samples, first and third weeks, March through November; double samples, third week, December through February.

Funk Forest: single samples, second and fourth weeks, March through November; double samples, second week, December through February.

To obtain the ground samples, a metal ring, 7.5 cm high and covering 0.1 m^2, was forced into the ground until its top was level with the surface. The surface litter was placed in a paper bag or other container, and the soil to the bottom of the ring was put in a cloth sack. The litter was placed by the research assistant into a Berlese funnel and left for approximately a week. At the end of this period search was made in the litter for larger specimens that did not go through the screen, and the alcohol specimens were set aside for later identification and counting. The sacks containing the soil collection were placed, when wet, in a refrigerator to dry out and then sorted over by hand, usually by the Woods Custodian, to remove the animals present. Counts of animals in the litter and soil were combined.

The *herb collections* consisted of 48 sweeps with a standard-sized insect net (diameter 33 cm, with a sack 61 cm deep) of the herbaceous plants and young trees and shrubs in the herb stratum. The schedule was as follows:

Research assistant: William Trelease and Brownfield Woods, first and third weeks, April through October.

Woods Custodian: William Trelease and Brownfield Woods, second, fourth, and fifth weeks, April through October; first and third weeks, March and November; third week only, December through February, often omitted. Funk Forest, second and fourth weeks, March through November; second week, December through February, often omitted.

The herb stratum is nearly continuous with an average height of 0.5 m.

The shrub collections were made on the same schedule as the herb sweepings. Forty-eight sweeps with the insect net were taken lengthwise of the branches of shrubs and the lower branches of trees. Attention was given not to take excessive sweeps of the abundant pawpaw and to include a half-dozen sweeps each of Ohio buckeye and basswood. Although shrubs are scattered singly or in clumps, their

foliage extends over a greater vertical distance so that their average volume per unit area may approximate that of the herbs.

Collections were usually taken in late morning or early afternoon but were not taken during times of rain or when the vegetation was wet. Variations in moisture conditions, temperature, and wind velocity may have affected the size of the collections somewhat (Weese, 1924; Blake, 1926; Shelford, 1951a).

The insects and spiders were anesthetized while in the sweep net and then transferred to a paper bag. The bags were stored in a refrigerator when necessary, but the material was usually sorted over and the animals placed in vials within a day or two after collecting.

Practically all identifications and counting were done by the research assistants. After counting, the specimens were stored in alcohol for future reference. The census data were first put onto work sheets and later calculated as densities per square meter. Later, monthly summaries were made that gave averages of the weekly counts and combined all the strata. Shelford (1951a) has estimated that measurements of population size obtained in this manner may represent only about one-half of the number of individuals present. While the accuracy of the conversion to absolute density per unit area is at best approximate, the same procedure was used throughout the study so that the fluctuations from month to month and from year to year should have meaning.

Great care was taken at the beginning of the investigation to obtain accurate identification of the specimens by specialists. A reference collection was established and an annotated list prepared giving the recognition marks of each species or other taxon. Each assistant adhered to this standard, but there was doubtless some variation in their abilities to make accurate determinations. At the end of the series, in 1972, samples of many of the species were selected from the collections over the later years and again submitted to specialists. The identification of insect species was, with minor exceptions, found to be consistently accurate. The spiders and ants, however, presented difficulties, and species names will be used sparingly. Immature forms often presented difficulties, and sometimes counts of two closely similar species have been combined.

Reliability of Estimates

Shelford (1951a) discussed in detail the reliability of the sampling procedure. In order further to evaluate the accuracy of the sampling, a different investigator (Graves, 1953) made collections of

insects from the herbs and shrubs using the same technique for comparison with the regular collector. The collections were made throughout the year at a different location within William Trelease and Brownfield Woods. Comparison of weekly estimates of population size of 14 species by the two collectors showed differences of less than 100 per cent in 35.5 per cent of the cases, between 100 and 300 per cent in 37.5 per cent of the cases, and over 300 per cent in 26.9 per cent of the cases (Figs. 11, 12). Comparison of monthly averages of population sizes showed differences of less than 100 per cent in 63.3 per cent of the cases, between 100 and 300 per cent in 24.1 per cent of the cases, and over 300 per cent in 12.5 per cent of the cases. Comparison of seasonal (June through September) estimates of mean population sizes showed the closest agreement — differences of less than 100 per cent in 74.0 per cent of the cases and between 100 and 266 per cent in 25.9 per cent of the cases (Fig. 13). The differences in population estimates obtained by the two collectors are ascribed to variations in the vegetation and terrain where the collections were made, different days when collections were taken, chance inclusion or omission of semi-colonial species, weather conditions, and minor differences in procedures. These comparisons indicate that the annual and monthly totals used in this monograph are good population estimates within 100 to perhaps 250 per cent. Fluctuations of less than 200-300 per cent may represent sampling error.

Population Variables

In consideration of the above checks, two population variables were selected for analysis. The *yearly index* (A_y) was calculated by summing the average populations (number m^{-2}) each month throughout the calendar year. The yearly index may be converted to mean monthly populations by dividing by 12.

Monthly populations from January to emergence from winter dormancy in the spring represent survival over the preceding winter and the breeding population. High monthly populations during the summer months include the increments of reproduction over mortality, and decreasing populations during the autumn represent the survival from weather, disease, predators, and competition. The size of the *maximum monthly population* (A_m) may be a sensitive and responsive index of how the prevailing environmental conditions have affected reproductive success.

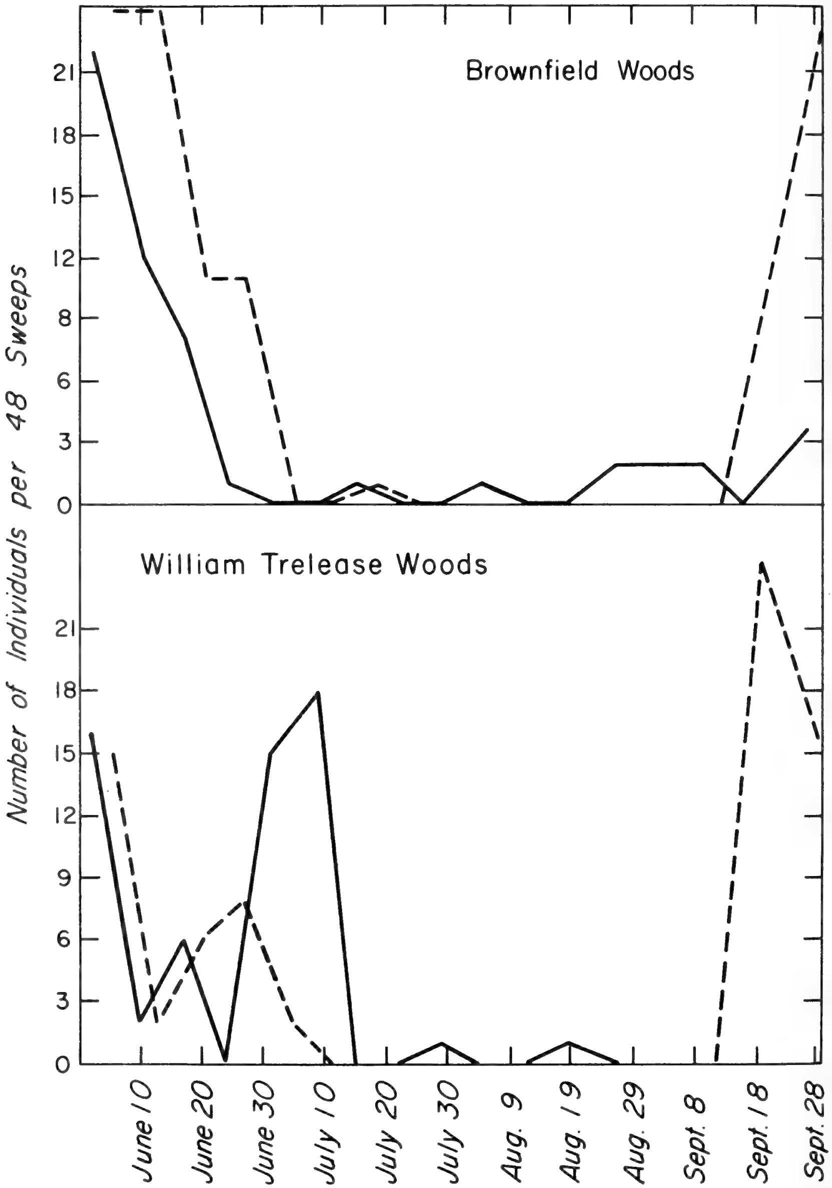

Fig. 11. Weekly variations in population of the fly *Sympycnus lineatus* during 1952 as determined by the project collector (solid line) and by Graves (1953) (broken line).

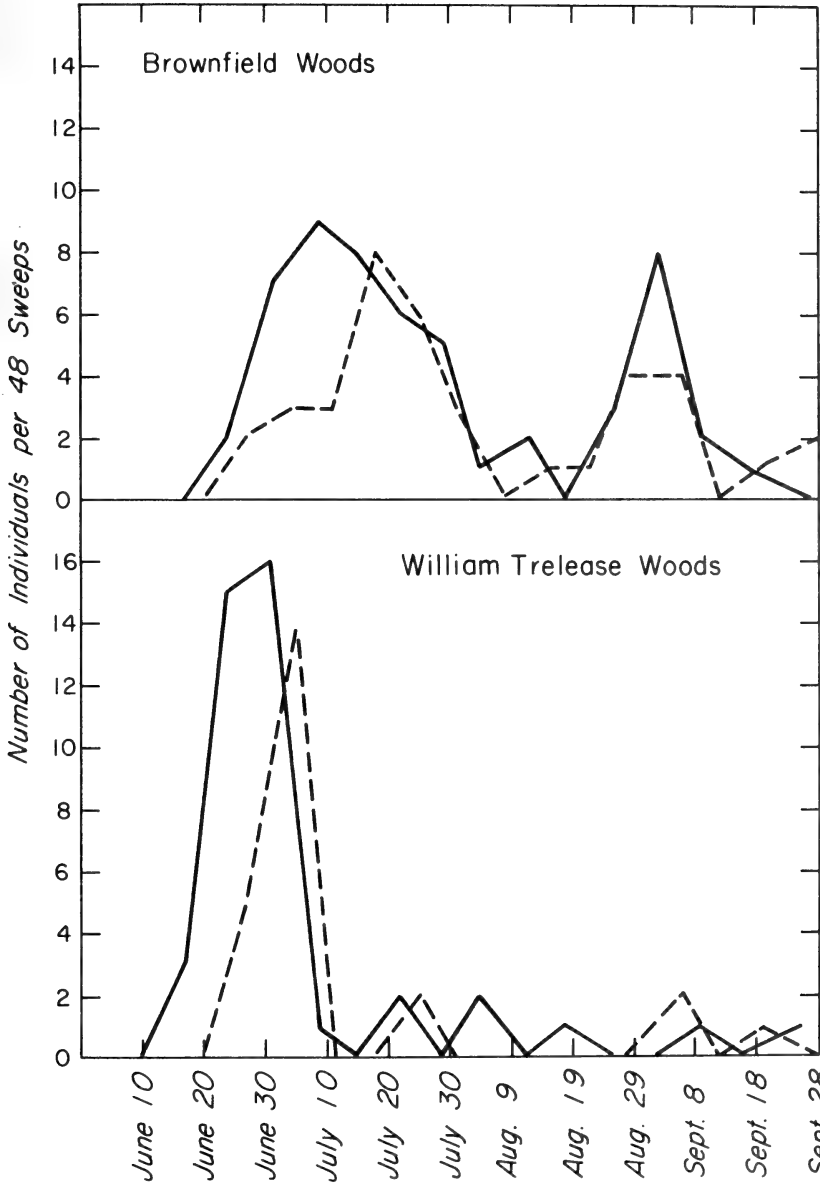

Fig. 12. Weekly variations in population of the fly *Pseudogriphoneura crevecoeuri* during 1952 as determined by the project collector (solid line) and by Graves (1953) (broken line).

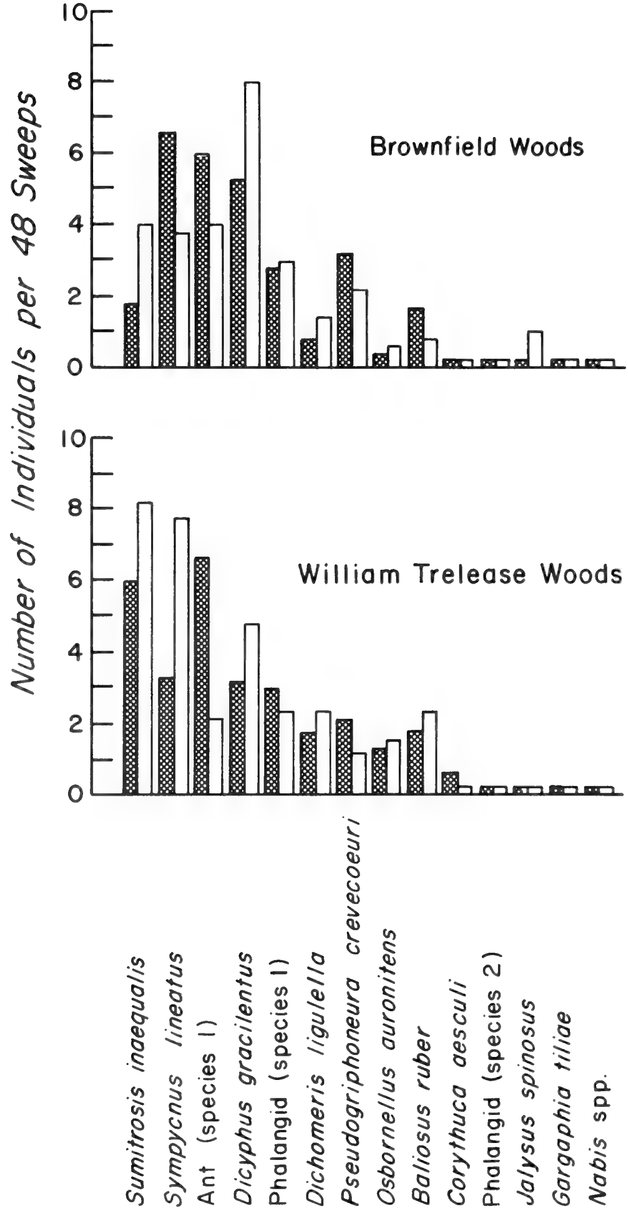

Fig. 13. Average seasonal populations during 1952 as determined by the project collector (dark bars) and by Graves (1953) (light bars).

6. Total Woods Fauna and Populations

Taxa and Mean Population Sizes

The fauna in the collections at William Trelease Woods consist of representatives of 6 classes, 15 orders, 42 families, 49 genera, and 48 recognized species (Table 5). The predominant taxa in descending rank of population size are beetles, flies, spiders, homopterans, and snails and slugs.

The large standard deviations shown in Table 5 for both the yearly index and average monthly maximum indicate that fluctuations from year to year are very large. The standard deviations are frequently larger than the averages, which indicates that the distribution of yearly populations are skewed; that is, they are closely compacted between the average and zero but extend in a long tail to very large populations during some years. In this type of distribution (i.e., log normal) the mean as calculated is greatly influenced by rare but very large events, and perhaps the median would have been more appropriate. However, we are not here concerned in explaining the differences in population levels of different taxa but in analyzing the causes for the wide yearly fluctuations.

The month of highest average population throughout the period of censusing, *month of average maximum,* is indicated. During some years the maximum monthly population came either earlier or later. The *average monthly maximum* is the mean of the maximum monthly population each year, regardless of the month in which it occurred.

Yearly Cycle

The total population in William Trelease Woods, averaged by months for the 38 years of study, reaches its peak in September (Fig. 14). A smaller peak occurs in May followed by a decline in June, July, and August, the hottest part of the year. Different taxa, however, reach peak populations at different times (Table 5). The actual sizes of

Table 5. Taxa censused and mean populations (± standard deviations) ir William Trelease Woods

Taxa	Years of record	Yearly index[1]	Month of average max.[1]	Average monthly max.[1]
Total woods population	38	7493 ± 3858	Sept.	1227 ± 668
Herbs and shrubs	38	1846 ± 687	Sept.	428 ± 181
Ground	38	5640 ± 3333	Nov.	1030 ± 600
ARACHNIDA (harvestmen, spiders)				
OPILIONES (harvestmen)				
Ischyropsalidae	23	32.0 ± 25.8	July	12.2 ± 10.0
ARANEAE (spiders)				
Total	26	743 ± 479	Sept.	142 ± 93
Herbs and shrubs	35	213 ± 102	Sept.	54.7 ± 24.6
Araneidae				
Mangora gibberosa (Hentz) and *M. maculata* Keyserling	37	31.6 ± 34.1	July	15.9 ± 16.3
Tetragnathidae				
Tetragnatha extensa (Linnaeus)	35	8.2 ± 12.2	Nov.	4.3 ± 6.2
Hahniidae				
Hahnia cinerea Emerton and *Neoantistea agilis* (Keyserling)	37	19.7 ± 22.5	Sept.	7.4 ± 7.6
Salticidae				
Zygoballus bettinii Peckham and *Z. nervosus* Peckham	37	11.6 ± 9.8	Sept.	4.3 ± 3.1
EUCRUSTACEA (crustaceans)				
ISOPODA (isopods)				
Oniscidae (woodlice, sowbugs)				
Tracheoniscus rathkei Brandt	38	113 ± 104	July	40.6 ± 33.7
DIPLOPODA (millipedes)				
Total	36	357 ± 476	July	104 ± 131
POLYDESMIDA				
Polydesmidae				
Scytonotus granulatus (Say)	36	48.1 ± 76.8	July	22.6 ± 35.5
Eurydesmidae				
Fontaria virginiensis (Drury)	38	84.8 ± 179	Feb.	38.4 ± 80.0
CHORDEUMIDA				
Cleidogonidae				
Cleidogona caesioannulata (Wood)	24	38.2 ± 61.5	Dec.	19.1 ± 32.6
CHILOPODA (centipedes)				
GEOPHILOMORPHA	38	316 ± 248	Apr.	67.2 ± 45.9
Geophilidae	24	222 ± 155	Apr.	54.6 ± 34.4

Table 5 (Continued)

Taxa	Years of record	Yearly index[1]	Month of average max.[1]	Average monthly max.[1]
INSECTA (insects)				
ORTHOPTERA	24	32.1 ± 19.2	July	11.5 ± 7.2
Phasmatidae (walking-sticks)				
Diapheromera femorata (Say)	23	3.4 ± 2.6	July	1.8 ± 1.3
Gryllidae (tree crickets)				
Oecanthus angustipennis Fitch	38	4.6 ± 8.8	June	2.6 ± 5.0
HEMIPTERA	24	354 ± 160	Sept.	72.7 ± 35.6
Reduviidae (assassin bugs)				
Zelus exsanguis (Stål)	38	8.7 ± 9.6	Sept.	4.3 ± 4.4
Nabidae (damsel bugs)				
Nabis spp., adults and nymphs	14	58.2 ± 35.6	Aug.	21.7 ± 16.1
nymphs only	23	27.8 ± 31.8	Aug.	9.3 ± 8.1
Tingidae (lace bugs)				
Gargaphia tiliae (Walsh)	38	34.4 ± 53.2	Sept.	14.8 ± 24.3
Corythuca aesculi Osborne and Drake	38	35.9 ± 51.5	Apr.	15.3 ± 20.9
Miridae (leaf bugs)				
Lygus lineolaris (Palisot de Beauvois)	38	45.8 ± 41.7	Nov.	21.6 ± 20.5
Horcias dislocatus (Say)	38	2.4 ± 3.1	June	1.5 ± 1.7
Dicyphus gracilentus Parsh	38	32.9 ± 42.0	Aug.	16.7 ± 27.0
Lygaeidae (chinch bugs)				
Blissus leucopterus (Say)	38	74.1 ± 154	Dec.	32.1 ± 55.0
Berytidae (Neididae) (stilt bugs)				
Jalysus spinosus (Say)	38	6.0 ± 4.5	Sept.	2.6 ± 1.7
HOMOPTERA	24	542 ± 214	Oct.	170 ± 106
Cicadellidae (leafhoppers)				
Osbornellus auronitens Provancher	28	3.8 ± 3.8	Aug.	2.2 ± 2.4
DIPTERA				
Total	24	1380 ± 1016	May	298 ± 230
Larvae, excluding Tipulidae	24	862 ± 850	May	229 ± 210
Tipulidae (crane flies)				
Adults	38	19.7 ± 14.4	June	7.3 ± 5.4
Larvae	38	51.2 ± 62.4	May	22.0 ± 26.2
Dolichopodidae (long-legged flies)				
Sympycnus lineatus Loew	25	27.1 ± 19.9	Sept.	12.3 ± 10.7
Lauxaniidae				
Pseudogriphoneura crevecoeuri (Coquillett)	38	9.9 ± 19.8	July	5.9 ± 11.6
Chloropidae				
Thaumatomyia glabra (Meigen)	38	2.4 ± 2.4	June	1.2 ± 1.0
Drosophilidae (fruit flies)				
Drosophila quinaria Loew	38	7.8 ± 11.4	Sept.	3.8 ± 5.9

Table 5 (Continued)

Taxa	Years of record	Yearly index[1]	Month of average max.[1]	Average monthly max.[1]
LEPIDOPTERA				
Total	24	206 ± 194	July	53.2 ± 49.3
Larvae	24	172 ± 179	May	46.2 ± 41.6
Gelechiidae (moths)				
Dichomeris ligulella Hübner	38	5.3 ± 7.9	July	3.1 ± 5.7
COLEOPTERA				
Adults and larvae	24	2662 ± 1119	Nov.	537 ± 364
Larvae, excluding *Ptilodactyla* spp.	24	399 ± 440	June	100 ± 118
Carabidae (ground beetles)				
Adults	24	96.6 ± 96.3	Jan.	24.8 ± 29.7
Staphylinidae (rove beetles)				
Adults	24	714 ± 801	Aug.	230 ± 347
Anthicidae				
Notoxus monodon Fabricius and *N. bicolor* Say	38	76.6 ± 118	Mar.	42.6 ± 77.1
Ptilodactylidae				
Ptilodactyla serricollis (Say)				
Adults	38	4.5 ± 10.9	June	3.4 ± 7.5
Larvae	38	75.0 ± 98.5	Sept.	36.3 ± 48.9
Cucujidae				
Telephanus velox Haldeman	38	179 ± 246	Nov.	102 ± 227
Lathridiidae				
Melanophthalma spp.	38	177 ± 184	Nov.	65.7 ± 133
Chrysomelidae (leaf beetles)				
Diabrotica undecimpunctata howardi Barber	38	3.2 ± 4.1	Apr.	2.2 ± 3.0
Acalymma vittata Fabricius	38	18.2 ± 25.6	May	9.7 ± 19.2
Cerotoma trifurcata (Forester)	19	83.6 ± 82.8	Jan.	30.2 ± 25.2
Baliosus ruber (Weber)	38	5.9 ± 8.5	May	2.7 ± 3.2
Sumitrosis inaequalis (Weber) and *S. rosea* (Weber)	38	56.0 ± 135	Sept.	22.4 ± 59.6
Curculionidae (snout beetles)				
Apion spp.	38	3.1 ± 3.8	June	1.8 ± 2.0
Idiostethus tubulatus (Say) and *I. subcalvus* (LeConte)	38	17.3 ± 20.2	May	10.7 ± 12.9
Lechriops oculatus Say	38	5.3 ± 5.9	Sept.	2.4 ± 2.2
Nonforest species, total	38	2084 ± 10730	Mar.	100 ± 102
HYMENOPTERA				
Total, excluding Formicidae	5	153 ± 40.6	June	29.2 ± 6.5
Formicidae (ants)				
Total	26	804 ± 496	May	291 ± 218
Herbs and shrubs only	38	95.1 ± 47.3	July	32.9 ± 19.9
Aphaenogaster rudis Emery	34	71.9 ± 89.0	May	41.9 ± 66.7
Ponera pennsylvanica Buckley	27	215 ± 176	June	92.4 ± 71.8

Table 5 (Continued)

Taxa	Years of record	Yearly index[1]	Month of average max.[1]	Average monthly max.[1]
GASTROPODA (snails, slugs)				
Total	24	509 ± 565	Sept.	171 ± 345
BASOMMATOPHORA				
Ellobiidae				
Carychium exile H.C. Lea	38	74.8±160	Sept.	43.8 ± 134
STYLOMMATOPHORA				
Polygyridae				
Mesodon thyroidus (Say) and *M. pennsylvanicus* (Green)	38	26.6 ± 38.6	June	12.5 ± 15.8
Zonitidae				
Retinella indentata (Say)	38	95.9 ± 104	Sept.	28.5 ± 26.3
Endodontidae				
Hawaiia, Striatura, Punctum spp.	38	31.3 ± 66.6	Sept.	16.6 ± 42.6
Haplotrematidae				
Haplotrema concavum (Say)	38	29.9 ± 34.4	Sept.	11.7 ± 13.2
Pupillidae				
Vertigo, Columella spp.	38	32.8 ± 42.6	Sept.	15.6 ± 27.4
Succineidae				
Succinea avara Say	38	27.0 ± 71.2	Sept.	9.7 ± 25.2
Limacidae				
Deroceras spp.	38	12.1 ± 25.7	June	6.7 ± 11.4

[1] For explanation, see p. 25.

peak populations are underestimated in this monograph because they are monthly averages. Shelford (1951a) described weekly variations in numbers of some taxa where the data permitted. For instance, a phorid fly, *Parasphinophora multiseriata* Ald., attained a peak population of over 65 in the week of July 19, 1937, although the monthly average was only 26.

Minimum populations occur during the winter months when most animals are in the surface litter, in or under decaying logs, or in the ground. A few spiders may find shelter among dry leaves clinging to the trees or in bark crevices. Most forms will tolerate moderate freezing. Blake (1926) states: "Animals of all sorts, mollusks, myriapods, arachnids and insects, when thawed out of the leaves or the solid masses of frozen soil moved about actively and seemingly with vitality unimpaired. There was nothing in their appearance or behavior to indicate any marked winter mortality." Extreme low temperatures, however, cause mortality and some species move

between litter and ground and between different depths in the ground to keep below the frost line (Dowdy, 1944). On warm days some individuals may be active above ground or flying.

Our data show that animals inhabiting the leaf litter and ground stratum average 3.0 times as abundant throughout the year as do those in the herbs and shrubs (Fig. 14). From late spring to early autumn, when foliage is present, they are still 2.4 times as numerous. The mean monthly population for all strata throughout the year is over 600 individuals.

Considering only insects and spiders, Weese (1924) found highest populations in the leaf litter on the ground surface except during early October, when larger numbers occurred in the herb and shrub strata because of the influx into the woods of insects from the forest margin and surrounding farmland. These species, however, quickly descended into the leaf litter and ground to hibernate. They appeared again in large numbers in the herb and shrub strata in late April and May on their way out of the woods. The curves in Fig. 14 do not show this phenomenon.

Yearly Fluctuations in the Three Woods

Fluctuations in the yearly index and the maximum monthly population agree closely (Fig. 15). The total population at William Trelease Woods shows an extended high from 1944 through 1953, peaking in the years 1945-47, with smaller peaks in 1960-61, 1965, and possibly approaching a peak in 1971. These same peaks occur separately in the herb and shrub and in the ground populations, although the 1960-61 and 1965 peaks in the ground population reach only half the size of the 1944-53 peak.

Figures were drawn for all species to compare fluctuations in the yearly index in the three woods, but only a few representative ones from different major taxa are shown (Figs. 16-22). There is considerable agreement among the three woods as to when peak and minimal populations were attained, but these are often off by one or sometimes two years. General trends in population over consecutive years are similar, although occasionally one woods does not agree with the other two. There is no consistent variation in absolute density of species among the woods, although an occasional species was persistently more abundant in one woods than another. If one disregards differences between areas or years where population ratios are less than 2-3 to 1, as owing to sampling error, then the fluctuations in population size in any one woods are representative of all three.

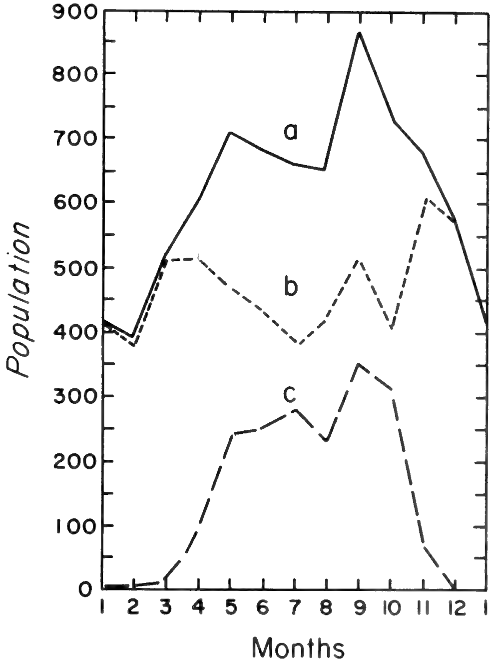

Fig. 14. Yearly cycle at William Trelease Woods of mean monthly (a) total woods population, (b) ground and litter population, and (c) herb and shrub population of animals.

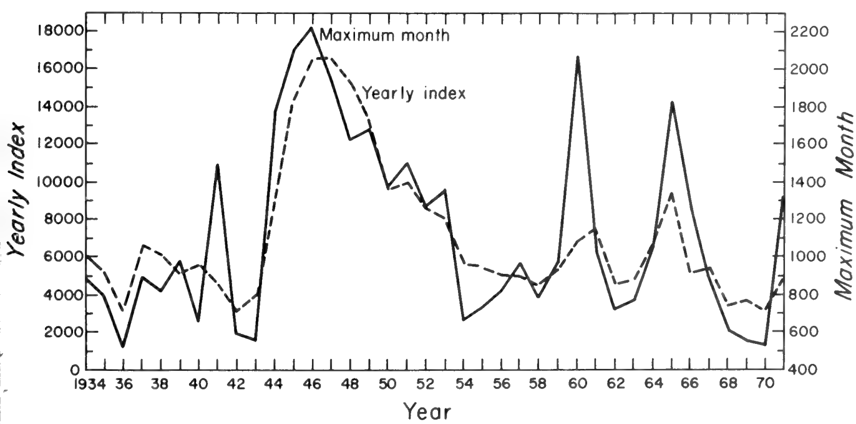

Fig. 15. Yearly fluctuations of two indices of total woods populations in William Trelease Woods.

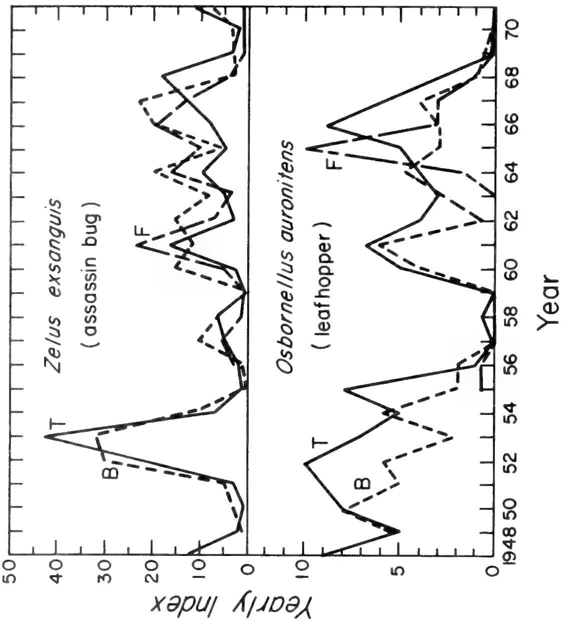

Fig. 17. Population fluctuations in William Trelease Woods (T), Brownfield Woods (B), and Funk Forest (F).

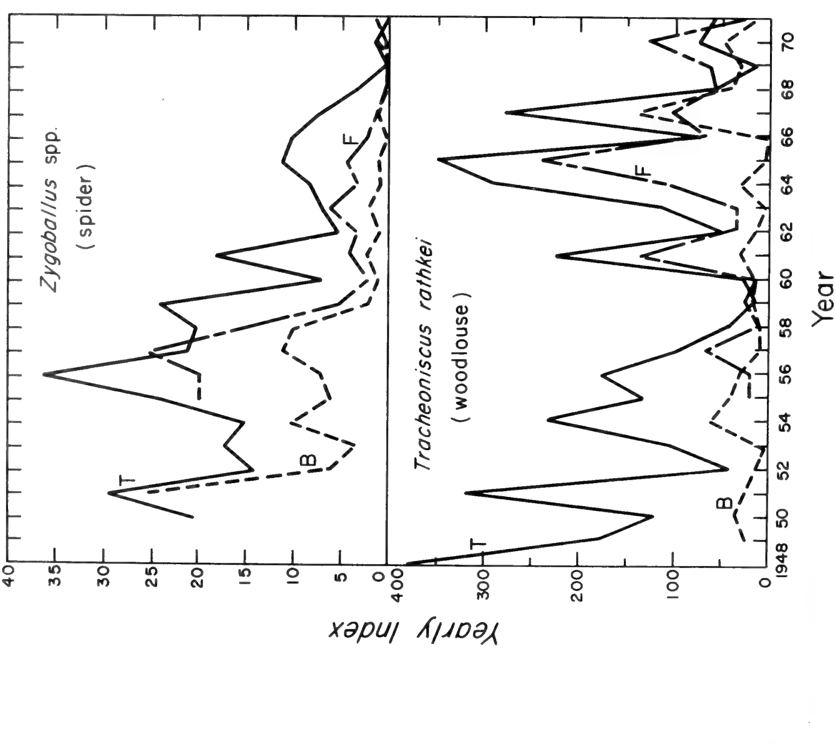

Fig. 16. Population fluctuations in William Trelease Woods (T), Brownfield Woods (B), and Funk Forest (F).

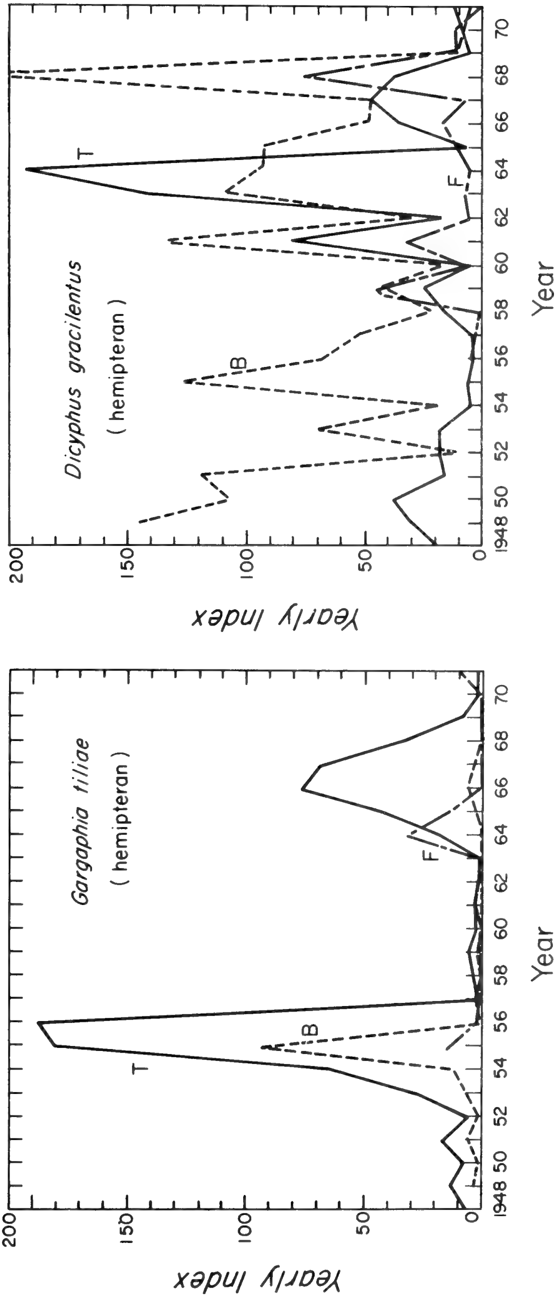

Fig. 18. Population fluctuations in William Trelease Woods (T), Brownfield Woods (B), and Funk Forest (F).

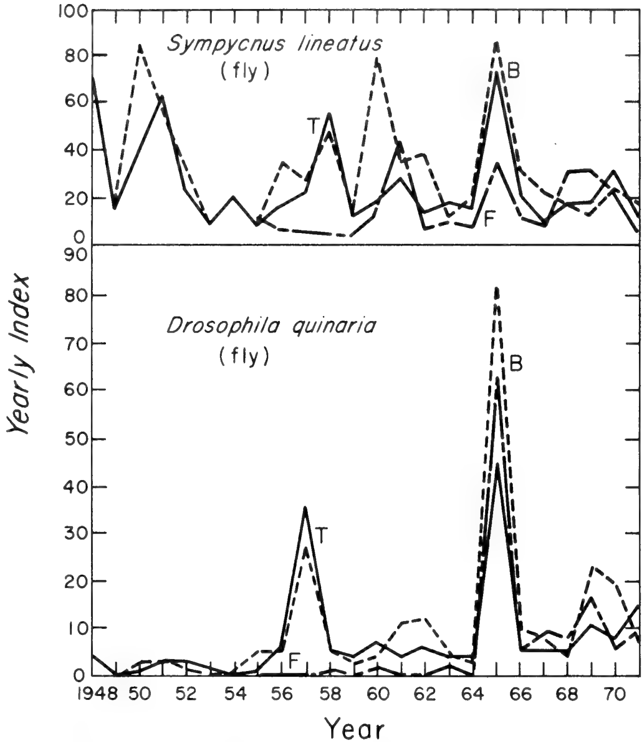

Fig. 19. Population fluctuations in William Trelease Woods (T), Brownfield Woods (B), and Funk Forest (F).

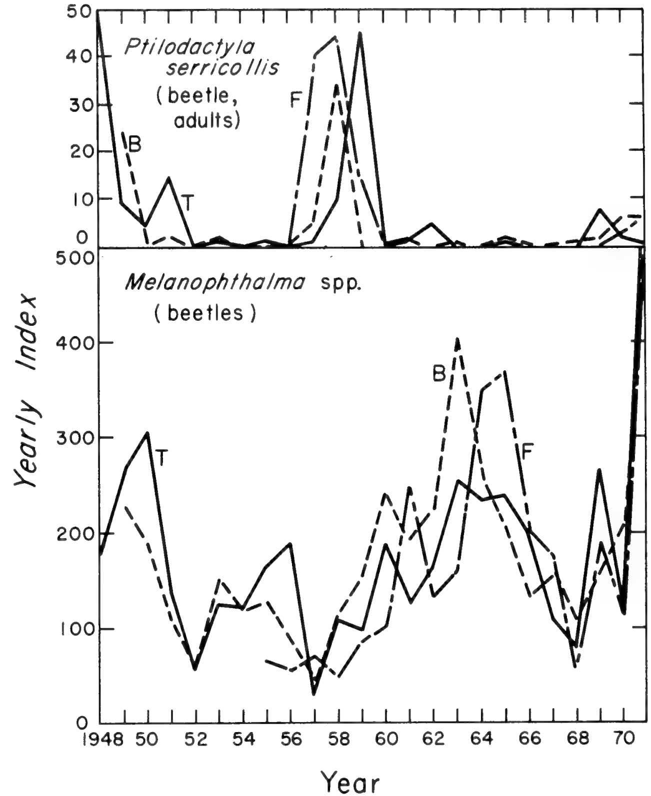

Fig. 20. Population fluctuations in William Trelease Woods (T), Brownfield Woods (B), and Funk Forest (F).

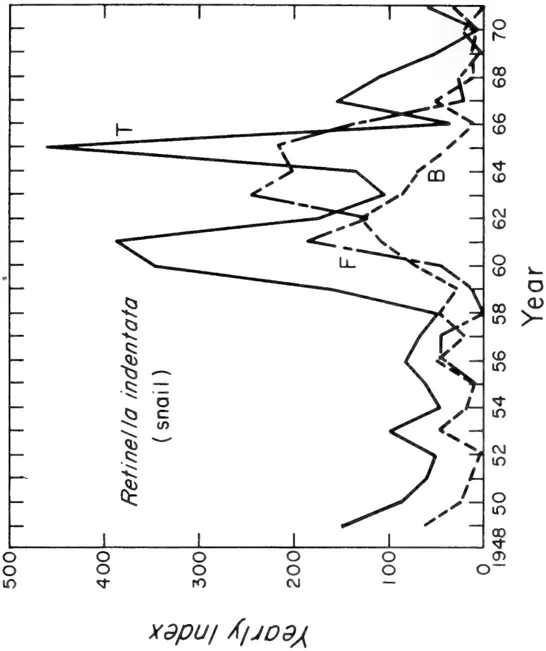

Fig. 22. Population fluctuations in William Trelease Woods (T), Brownfield Woods (B), and Funk Forest (F).

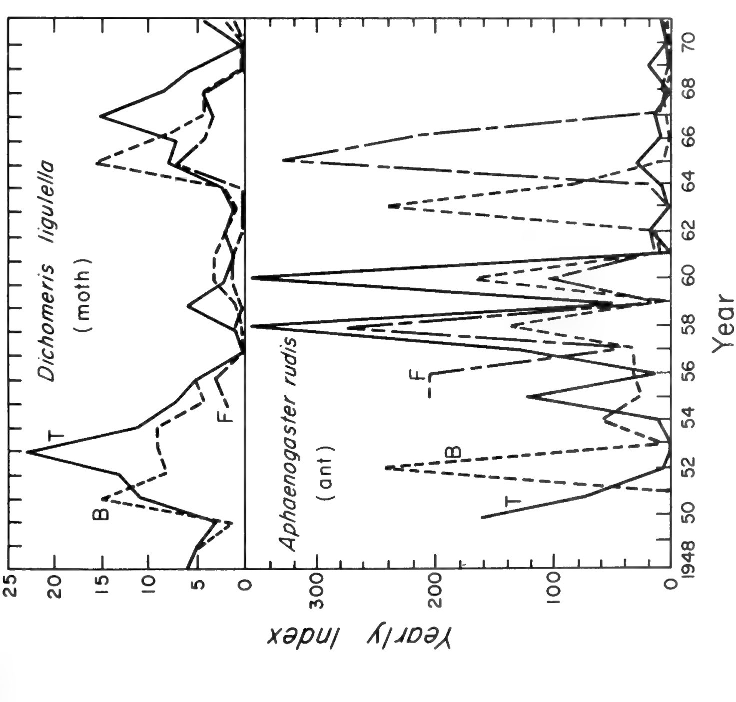

Fig. 21. Population fluctuations in William Trelease Woods (T), Brownfield Woods (B), and Funk Forest (F).

7. Multiple Regression Analysis

In order to determine the effect of fluctuations in weather and other factors on yearly population sizes of the various taxa, use was made of multiple regression equations. The "independent variables" are those listed in Table 3; the "dependent variables" are the yearly index (A_y) and the maximum monthly population each year (A_m). Computer programs were obtained from the SOUPAC library of the Department of Computer Science, University of Illinois.

Procedures

Two procedures were used. In the backward elimination procedure (BEP), described by Draper and Smith (1966), a regression equation was first computed including partial regression coefficients and an F-value for each of the independent variables. The variable with the lowest F-value was then removed and a new regression computed. This process was repeated until the F-values for all the remaining variables were significant at the 0.05 per cent level. The final equation with all variables significant was considered the "best" regression equation. The multiple correlation coefficient for this equation is invariably lower than when all variables are included (Table 6), but the equation will predict population size within reasonable limits with the least amount of data input. It is a compromise between accuracy and the use of an impractical number of variables. This procedure was used only in the analysis of the William Trelease Woods data and not for all taxa.

In the stepwise multiple regression procedure, described by Efroymson (1960), significant variables are added one at a time so that a number of intermediate regression equations are obtained. A partial regression coefficient, and its reliability, may vary with each subsequent equation but represent the best value when the equation contains those particular variables. A variable is retained in the equation

Table 6. Example of backward elimination procedure, using data for the maximum monthly population of *Zelus exsanguis* (assassin bug)

Step	1	2	3	4	5	6	7	8	9	10	11	12
Multiple Correlation Coefficient	0.99	0.90	0.89	0.93	0.92	0.88	0.91	0.88	0.87	0.85	0.84	0.82
T_1	−22.9	−34.8	−34.8	−13.7	−13.4		−10.6					
T_2	−55.8	−70.5	−72.5	−33.7	−39.8	−40.8	−44.4	−40.5	−39.4	−37.8	−39.4	−36.2
T_3	2.5											
T_4	0.19	0.28	0.28	0.11	0.11	0.003	0.088	0.002				
T_5	0.39	0.50	0.51	0.24	0.28	0.29	0.31	0.28	0.28	0.26	0.28	0.25
T_6	−0.011											
T_7	−22.4	−35.0	−37.5	−22.2	−24.8	−30.7	−29.9	−27.8	−23.7	−25.0	−22.8	−20.4
T_8	0.40											
T_9	3.0											
T_{10}	0.18	0.27	0.29	0.17	0.19	0.24	0.23	0.22	0.18	0.20	0.18	0.16
T_{11}	−0.005											
T_{12}	−0.023											
T_{13}	−0.098											
P_1	−4.7	−4.2	−3.6	−1.5	−1.0							
P_2	11.7											
P_3	−0.99	−1.2	−1.2	−0.65	−0.63	−0.62	−0.66	−0.63	−0.50	−0.46	−0.40	−0.37
P_4	−0.51											
P_5	0.15											
P_6	−0.46	0.63	0.32	0.32	0.22							
P_7	−0.74	0.27		−1.6								
P_8	0.65	0.81	0.45	0.38	0.27		0.24					
P_9	−0.19	−0.38		−0.127								
P_{10}	0.27	0.25	0.24	0.12	0.11	0.063	0.064	0.064	0.059	0.062	0.056	0.038
P_{11}	0.05											
TP_1	−0.015	−0.017	−0.024	−0.010	−0.013	−0.011	−0.014	−0.012	−0.012	−0.011	−0.008	
TP_2	−0.17	0.024	0.023	0.008	0.007	0.004	0.006					
TP_3	−0.18	−0.012	−0.007	−0.006	−0.003							
S_1	1.0	1.2	1.3	0.38	0.36	0.48	0.52	0.49	0.44			
S_2	−0.036	−0.039	−0.044	−0.014	−0.015	−0.017	−0.020	−0.017	−0.014	−0.002		
U_1	−0.070	−0.045		−0.086								
U_2	0.10											
PP	0.089	0.21	0.22	0.040								

if it makes a significant improvement in "goodness of fit" or provides a reduction in variance of the dependent variable. A variable may be significant in an early step but, after several other variables are added to the regression equation, becomes insignificant. In this situation the stepwise procedure will remove the insignificant variable before adding an additional one. The final regression equation includes only those variables that remain significant. These variables were sometimes the same ones as obtained by the backward elimination procedure, but often they were different. The F-level taken for a variable to enter into an intermediate equation differed somewhat with the number of years of data available but varied from 4.120 to 4.540. The F-level taken to remove a variable from an equation varied from 3.500 to 4.400.

Interpretation of the Equations

The final equation in both procedures *predicts* the value of the dependent variable, population size, from a given set of significant independent variables. The partial regression coefficient of each variable indicates the change in population size as affected per unit change of that variable. The Y-intercept in the multiple regression equation is required for calculating the population size but has no particular biological significance. The multiple correlation coefficient (R) and the standard error of the estimate (indicated as $\pm$ *SEE*) give an evaluation of the overall extent to which population size depends on the measured variables and the closeness to which population size can be predicted. Deviations between the actual and predicted values were also calculated. The stepwise multiple regression was the procedure used more extensively and may be assumed for the values obtained unless otherwise stated.

Any effect on the equations as a result of the interrelations between the independent variables, shown in a preceding section (p. 19), could probably have been eliminated by undertaking a ridge trace analysis (Hoerl and Kennard, 1970a, b; Mauriello and Roskowski, 1974), but it is questionable whether the extra accuracy is justified. A factor analysis procedure was tried but abandoned because so many factors appeared important that considerable difficulty was experienced in reducing the number to a workable few. Perhaps the data would more properly have been treated by statistical linear prediction theory and time series analysis, but there are very complex problems involved in fitting models to time series data, and this procedure was not used.

A further difficulty is that my analysis presumes a linear or curvilinear relationship between population size and the environmental variables. Such a relationship may be true for only a portion of the range of the variable. The use of climographs by Shelford (1951a, b) shows, for instance, that populations may be highest at combinations of medium precipitation and ultraviolet radiation or temperature and may decrease as any one of these factors becomes extreme toward either maximum or minimum. The finding of significant relationships using multiple regression analysis suggests that the factor involved is important, but its effect on the population may be more intricate and complex than indicated. Likewise, the inability to find a significant relationship using multiple regression analysis may not mean that the particular factor is of no importance. Quite possibly the factor shows a positive correlation with population size under certain circumstances and a negative correlation under other circumstances, one effect canceling the other.

An attempt is made to show the relative importance of the different independent variables on population size by the number of times that they enter into the equations for each major taxonomic group. This is not altogether satisfactory as it disregards the relative size of the partial regression coefficients. Often it is possible to indicate whether the correlation is positive or negative, although the plus or minus sign as well as the size of the partial regression coefficient may depend in part on the step at which the variable enters into the computer procedure. Correlation is more difficult when both the value of a variable and its square enter into the equation, since they usually have opposite signs, but the variable squared generally has the greater quantitative influence on population size.

Equations for the yearly index ($A_y \pm SEE$) and monthly maximum populations ($A_m \pm SEE$) were calculated for each taxon for each of the three woods (see Appendix). Equations using the stepwise procedure for William Trelease Woods will be given for all the taxa because the record of measurement is longest for this area and is based on approximately twice the number of weekly collections. Equations for one of the other two woods (B = Brownfield, F = Funk) will be given in addition only when they have higher multiple correlation coefficients (R). Predictive equations obtained by the backward elimination procedure (BEP) will be given only when they have a correlation coefficient higher than that obtained by the stepwise procedure.

8. Population Fluctuations of Individual Taxa

Treatment of each taxon listed in Table 5 will include an analysis of (a) the yearly cycle of mean monthly populations, (b) fluctuations in the size of the maximum month's population over the years, (c) the predictive equations, and (d) the relative importance of the controlling factors.

The yearly cycle of mean monthly populations is based on data from William Trelease Woods only. The figures showing fluctuations from year to year are only for the maximum month's population but, as shown above (p. 35), these fluctuations agree closely with those for the yearly index. The figures are based on data from William Trelease Woods only for the years 1934 through 1948, on averages of the data from William Trelease and Brownfield Woods for 1949 through 1954, and on averages from William Trelease and Brownfield Woods and Funk Forest for 1955 through 1971.

Total Woods Populations

The yearly cycle of variations in mean monthly populations and fluctuations in population size from year to year have been discussed in Chapter 6. Predictive equations for the total populations in each woods are given in the Appendix. Only a few weather variables enter into these equations. This is not surprising, since weather affects different species in different, often contrasting, ways. The population size the preceding year, however, appears in nearly every equation and remains the most useful variable for predicting the size of the population the following year. Weather simply modifies this correlation somewhat by affecting mortality, especially overwinter, and reproduction.

Opiliones (Harvestmen)

There are at least two common species of harvestmen: *Leiobunum crassipalpe* Banks and *L. politum* Weed. Populations peak in July and

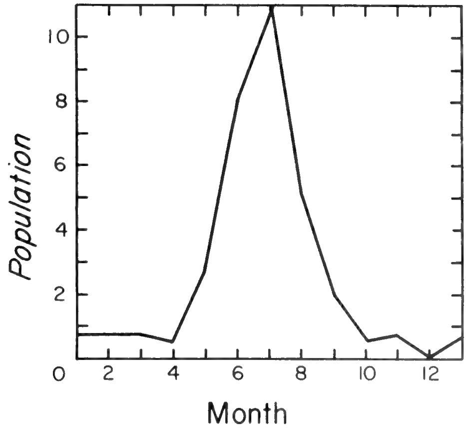

Fig. 23. Mean monthly populations of harvestmen.

small numbers may be found throughout the winter (Fig. 23). Phalangids also overwinter as eggs which hatch in the spring. Adults that overwinter lay eggs in April and May (Comstock, 1913).

Measurement of populations did not begin until 1949. A peak occurred in 1951, there followed low numbers from 1952 through 1957, after which there was a slow, irregular increase for the duration of the study (Fig. 24). It is of interest that the forest canopy was badly disturbed by the death of elm trees during the 1950s but has been recovering since. From the predictive equations (Appendix), it appears that harvestmen are favored by ample precipitation the previous year (P_6, P_9).

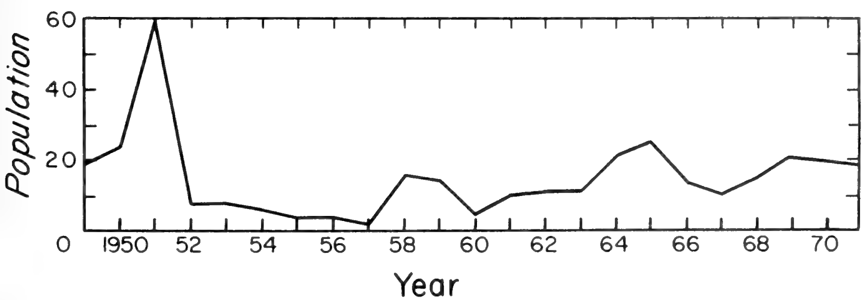

Fig. 24. Yearly fluctuations in maximum populations of harvestmen.

Araneae (Spiders)

Jones (1940) found 25 species abundant in William Trelease Woods and an additional 63 species of infrequent or incidental occurrence. Because of the difficulties of species recognition, especially as both adults and young were included in the counts, my analysis of population fluctuations has been made only by stratum, family, and genus. Davidson (1932), however, has shown how populations of 7 species varied seasonally in 1925-26.

Spiders have reduced populations during the winter when they mostly disappear from the herbs and shrubs (Fig. 25). Many species may pass the winter also as spiderlings within the egg-sac (Comstock, 1913). The number of spiders in the ground and litter is fairly constant throughout the year; this is well shown for the family Hahniidae,

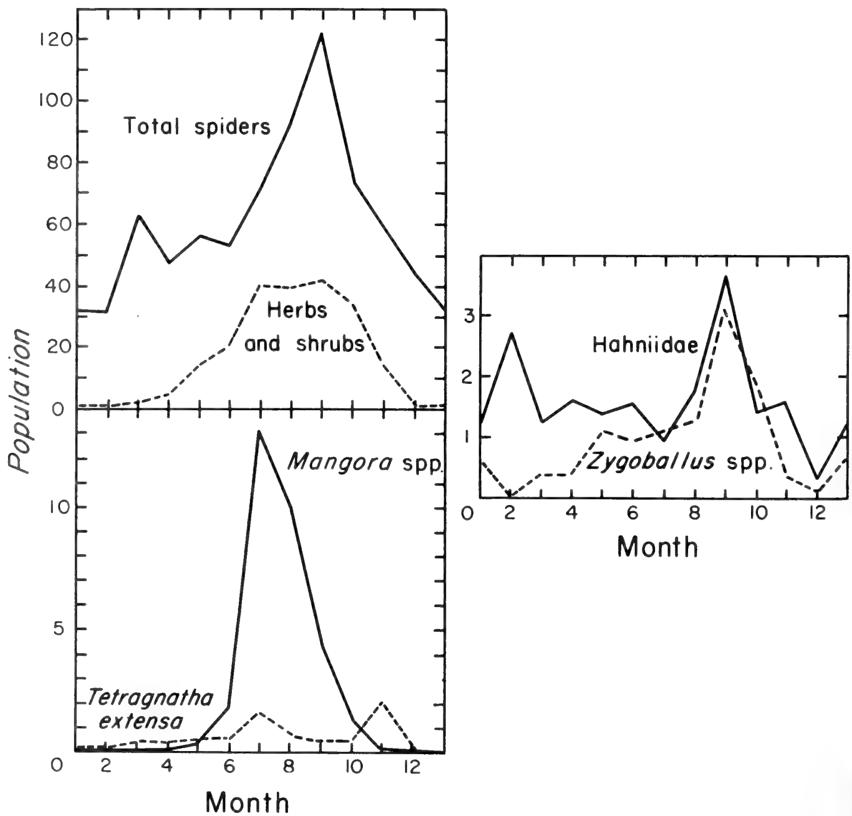

Fig. 25. Mean monthly populations of spiders.

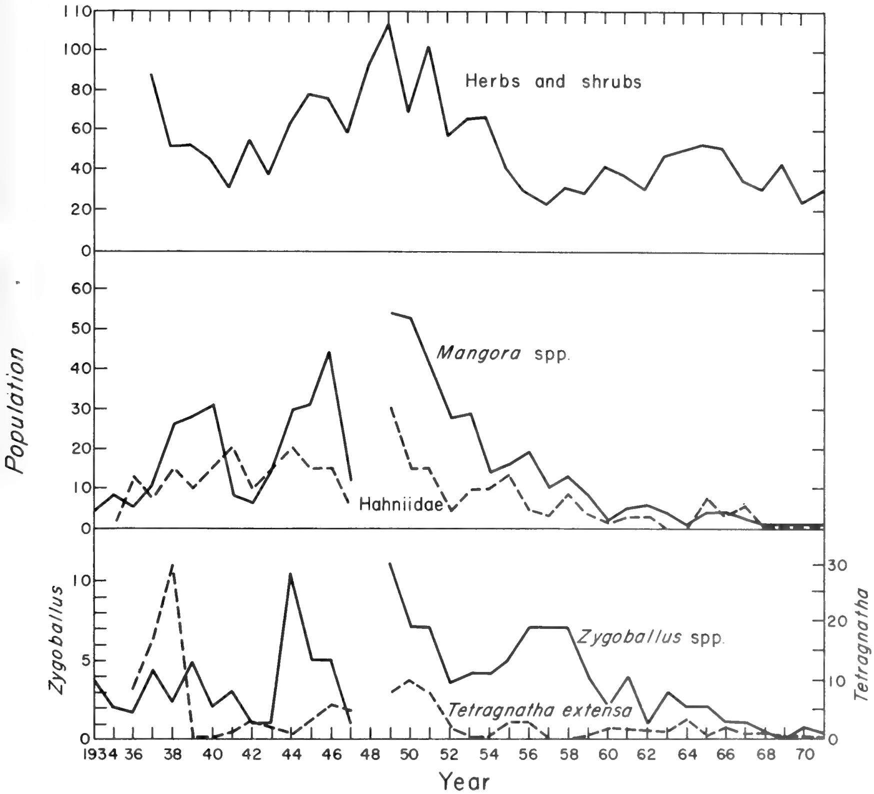

Fig. 26. Yearly fluctuations in maximum monthly populations of spiders.

which contains mainly ground inhabitants. The herb and shrub spiders reach their monthly peaks usually between July and September. Weese (1924) found only adults of *Tetragnatha* sp. at William Trelease Woods early in the season and only young in the autumn, with highest populations in November and December. Overwintering in this taxon may also take place above ground in bark crevices and other protected niches. He also found populations of *Mangora gibberosa* to reach their maxima in August and states that the species overwinters as eggs, hence their low numbers. According to Shelford (1951a), the vast majority of *Mangora* is *gibberosa*.

The total spider population in the herb and shrub strata was large between the mid-1940s and mid-1950s, and some species were also numerous in the late 1930s (Fig. 26). No identification of spider

taxa was made in 1948. The hahniids were absent from the collections in 1934 and 1935, reached a peak in the late 1940s, then declined until they disappeared again from 1969 through 1971. *Mangora* was never absent but shows a similar population surge over this 24-year period.

The size of the population the preceding year (PP) enters into every one of the predictive equations (Appendix). The most frequent weather variables in the equations are precipitation and temperature of the preceding year, especially during June, to which the spider population responds positively.

Isopoda (Woodlice, Sowbugs)

Smith (1928) reported *Procellio laevis* Latr. in William Trelease Woods, but the most common woodlouse is *Tracheoniscus rathkei.* The species shows a symmetrical cycle of abundance throughout the year with extreme high and low populations 6 months apart (Fig. 27). Since its life cycle covers 2 or more years, the considerable decrease in numbers recorded during the winter months is probably caused in large part by individuals seeking refuge in and under logs and deeper into the ground where collecting was not done. Pairing takes place in April and May, and there is only one brood per year (White, 1968).

Population size fluctuated extensively from year to year (Fig. 28), with low numbers prevailing through the first half of the 1940s followed by a peak in 1948. The best predictive equations were obtained for the Funk Forest populations (Appendix). Woodlouse populations appear to respond to variations in precipitation but in a confusing manner, perhaps depending on the time of year and whether or not the precipitation is excessive.

Diplopoda (Millipedes)

Seven species of millipedes are common in William Trelease and Brownfield Woods, each occupying a slightly different niche (O'Neill, 1967). They are less common at Funk Forest. Being ground animals, they may be found in good numbers at all times of year. Some species reach peak numbers in mid-summer, others in late winter or spring (Fig. 27).

In an intensive study of the life histories of two species in William Trelease and Brownfield Woods between 1944 and 1948, Hanson (1948) observed that both *Scytonotus granulatus* and *Pseudopolydesmus serratus* (Say) reproduced from March to May. The latter species

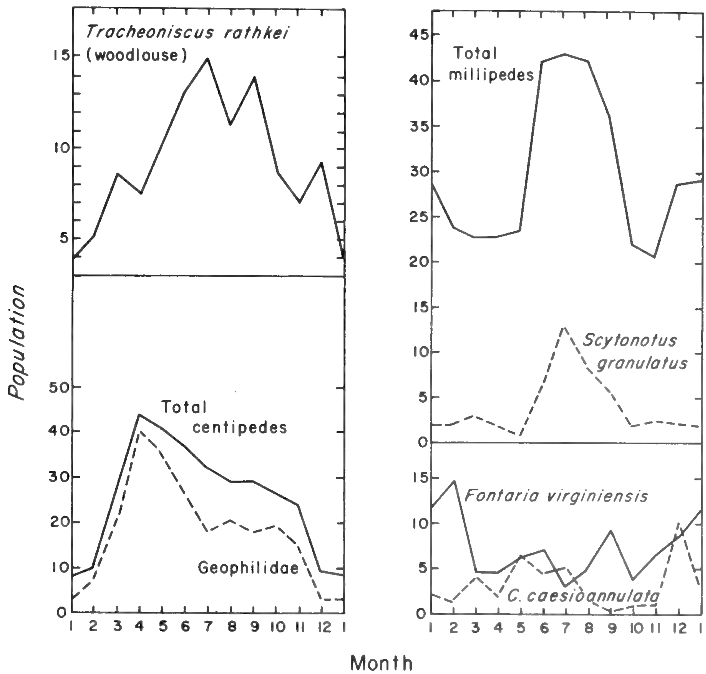

Fig. 27. Mean monthly populations of ground invertebrates.

had two separate, more or less independent, populations with the second population reproducing from June to August. Several developmental stages are passed through, with individuals of both species becoming sexually mature a year after hatching. Adults of *S. granulatus* reach a peak of numbers at the beginning of the reproductive season in March, while the large population of mid-summer consists of immature stages.

Millipedes were numerous during the early years with *S. granulatus* reaching peaks in 1938 and 1946 (Fig. 28) and *Fontaria virginiensis* in 1937-38, 1944, and 1948. *F. virginiensis* has occurred only irregularly since 1949 and in small numbers. We have not collected it at Funk Forest. On the other hand, *Euryurus erythropygus* (Brant), not included in the lists of any of the early workers, became quite common, particularly during the spring, at least by1952. These are closely related genera. *Cleidogona caesioannulata* likewise occurred only sporadically in the collections previous to 1949 but regularly thereafter. Weese (1924) did not find *E. erythropygus, P. serratus,* or *Abacion*

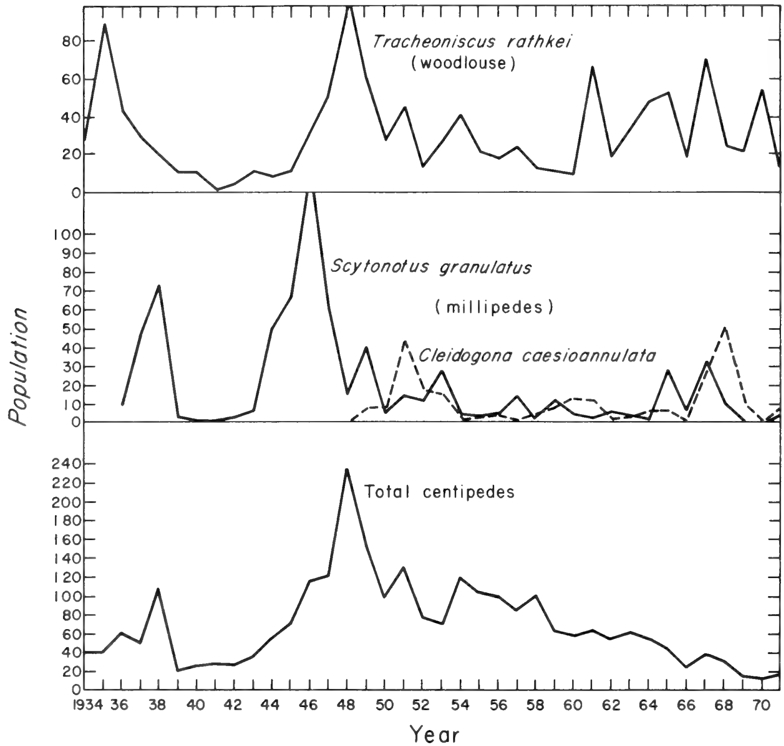

Fig. 28. Yearly fluctuations in maximum monthly populations of ground invertebrates.

lacterium (Say) during 1921-22, but *Narceus americanus* (Beauvois) occurred.

Yearly fluctuations were analyzed for only 2 species (Appendix). The size of the population the preceding year (PP) enters into 7 of the 11 equations. Superimposed on this variable are responses to a variety of temperature and precipitation variables but in no clearly defined manner.

Chilopoda (Centipedes)

At least 12 species of chilopods occur in William Trelease and Brownfield Woods (Table 7). Of these, *Bothropolys multidentatus* is the most numerous, with the possible exception of *Poaphilus kewinus*, a minute, soil-inhabiting geophilid. Species of chilopods were not distinguished in our counts, but most of them belonged to the Geophilidae.

Table 7. Species of Chilopoda (centipedes) recorded at William Trelease and Brownfield Woods (Auerbach, 1946)

Arenophilus bipunticeps (Wood)	*Neolithobius tyrannus* (Bollman)
Bothropolys multidentatus (Newport)	*Neolithobius voracior* (Chamberlin)
Geophilus rubens (Say)	*Otocryptops sexspinosus* (Say)
Linotenia chionophila (Wood)	*Poaphilus kewinus* (Chamberlin)
Linotenia fulva (Gager)	*Pokabius bilabiatus* (Wood)
Nadabius iowensis (Meinert)	*Sonibius numius* (Chamberlin)

Unlike most of the other ground-dwelling taxa so far discussed, centipedes reached maximum populations in the spring and declined in numbers during the rest of the year (Fig. 27). Auerbach (1951) explains that during early spring *Neolithobius voracior* and *B. multidentatus* occur chiefly in thick patches of damp leaf-mold; as summer approaches and relative humidity in the woods decreases, they move into decaying logs and stumps; and as the stratum dries in mid-summer, they move deeper into the logs or farther below the ground surface where they are not readily collected by our procedure. In these latter places they hibernate overwinter. Oviposition occurs chiefly in June and July and hatching in August and September. The young centipedes go into hibernation in November, and maturity is reached the next spring. Their life span may cover several years. Other species, as far as known, also follow this yearly cycle.

Except for minor fluctuations from year to year, the size of centipede populations increased to a peak in 1948 and declined steadily thereafter (Fig. 28). The predictive equations (Appendix) show that population size depends considerably on the size of the population the preceding year (PP). Auerbach (1949) showed experimentally that centipedes respond positively to moisture, but negative correlations with precipitation during June and July the preceding year (P_8) enter 4 times into the 8 equations and with total precipitation the preceding year (P_9) once. It may be that while centipedes respond positively to moist air, they are harmed or at a disadvantage in water-saturated ground resulting from heavy rains. A positive correlation with ultraviolet radiation from April through July (U_1) occurs 3 times in the equations.

Orthoptera

Fluctuations in the populations of the tree cricket, *Oecanthus angustipennis,* were followed throughout the study period but those of the walking-stick, *Diapheromera femorata,* only since 1949. Population

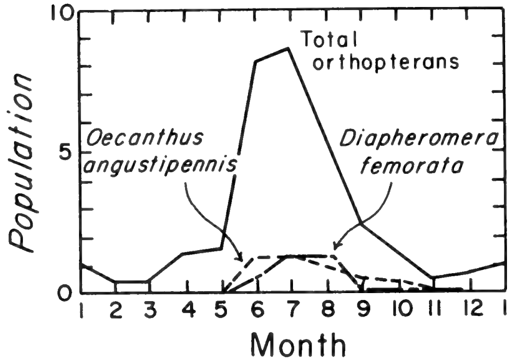

Fig. 29. Mean monthly populations of orthopterans.

counts are low, as the only individuals collected were those occurring in the tall shrubs and lower tree foliage.

Overwintering of these species is chiefly in the egg stage, hatching occurs in the spring, and a population peak from June through August (Fig. 29). The early individuals in the peak population of *D. femorata* in central Michigan were juveniles, as adults did not appear until the first week of August. The decline in numbers after August was attributed partly to predation and partly to movement upward into the tree stratum (Cantrall, 1943).

A major irruption of *O. angustipennis* occurred between 1945 and 1947. In 1950 there was an outbreak of miscellaneous other species of orthopterans (Fig. 30). The cause of these irruptions is not known. The size of the population the previous year (PP) is included in half of the predictive equations and precipitation in all but 3 (Appendix). The correlations with precipitation are mostly positive.

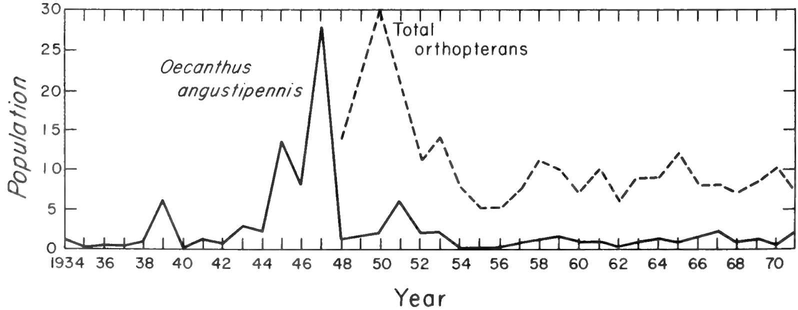

Fig. 30. Yearly fluctuations in maximum monthly populations of orthopterans.

Hemiptera

Weese (1924) identified 30 species of hemipterans in William Trelease Woods in 1921-22, but only 9 taxa are included in this study. *Horcias dislocatus,* which Weese did not record, was found in small numbers more or less regularly beginning in 1937.

Adults and nymphs of most species are present throughout the year but in largest numbers from May through October (Fig. 31). Knight (1941) states that the majority of mirid species overwinter in the egg stage except that it is characteristic of the genus *Lygus* to overwinter as adults. Adults of two species of *Dicyphus* have also been taken in hibernation. Adults of *D. gracilentus* were rarely found during the three winter months in our collections; the peak shown for January is based on a single large collection in 1964.

Species vary in having 1, 2, or more generations per year. *Jalysus spinosus* and *Zelus exsanguis* exhibit 2 peaks not only in William Trelease Woods but also in Brownfield Woods and Funk Forest, the first one in May and a larger one in September and October. *Blissus leucopterus* and *Lygus lineolaris* are not true forest forms, as during the summer they are out of the woods as pests on agricultural crops.

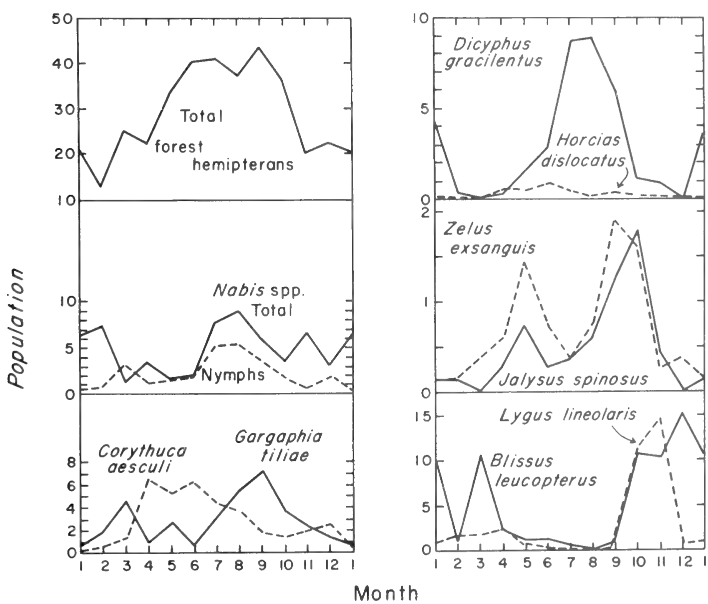

Fig. 31. Mean monthly populations of hemipterans.

According to Shelford and Flint (1943), the chinch bug, *B. leucopterus,* infests small grains in April and May and corn later. Here they have 2 or sometimes 3 generations. Adults return to the forest during the last warm days of autumn.

Both basswood, *Tilia americana,* and Ohio buckeye, *Aesculus glabra,* are prominent tree species in the woods, but I do not know how restrictive the two lace-bugs are in their feeding. The reverse fluctuations in populations of *Gargaphia tiliae* and *Corythuca aesculi* during the year (Fig. 31) suggest an adjustment between the two. Peaks of *G. tiliae* also occur in Brownfield Woods in March and September, but in Funk Forest there is no prominent spring peak and the main one occurs in August rather than September. Shelford (1951a) has shown that the spring peak is made up of adults, while the autumn peak represents the next generation. *C. aesculi* is uncommon in Brownfield Woods. In Funk Forest it reaches a large peak in March and a smaller one in August and September, apparently taking the place of *G. tiliae,* which is less common there. Weese (1924) found only small numbers of *C. aesculi* in William Trelease Woods in the early twenties but with a prominent peak in late April. He then claims that the lace-bug goes upward into the tree foliage, although he does not present evidence to show this. In 1934 Rice (1946) found this species reaching a peak of numbers April 24, mating by May 1, ovipositing on Ohio buckeye during early May, and having practically all young hatched by May 31. The inverse relation between *G. tiliae* and *C. aesculi* is further shown in their population fluctuations from year to year. During years when one species is high, the other is low, and vice versa (Fig. 32). In their predictive equations (Appendix)

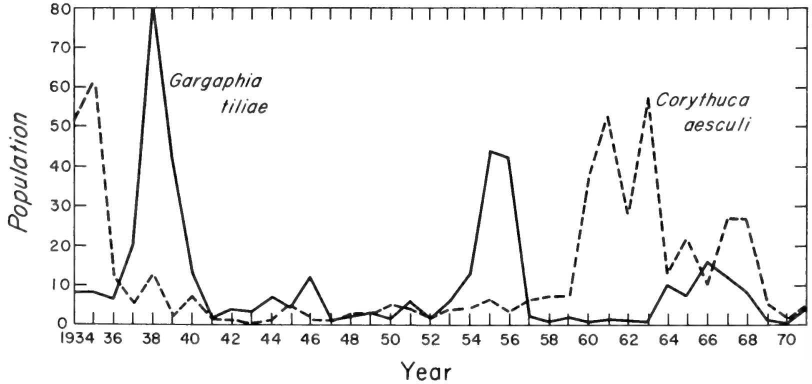

Fig. 32. Yearly fluctuations in maximum populations of hemipterans.

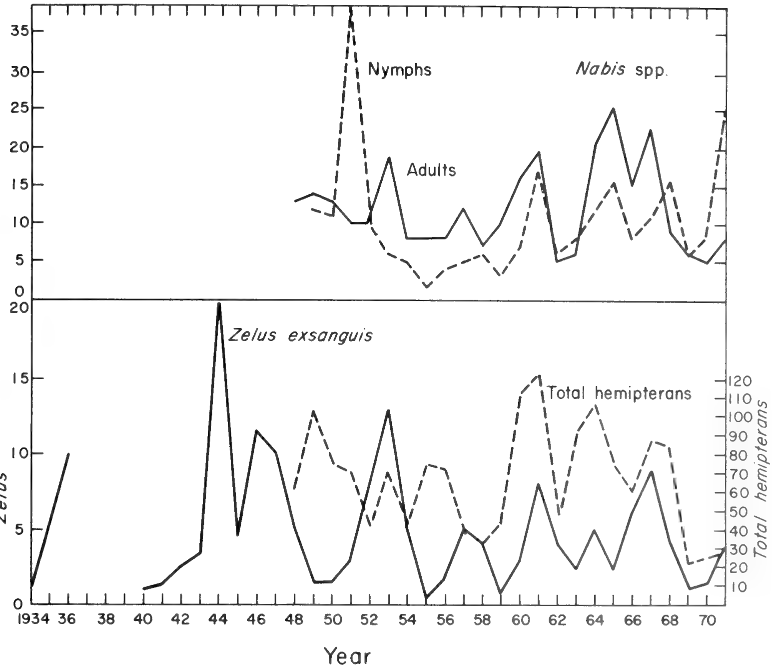

Fig. 33. Yearly fluctuations in maximum monthly populations of hemipterans.

G. tiliae shows a negative correlation with July temperature (T_3) and a positive correlation with July temperature squared (T_6), while the correlation of *C. aesculi* with these two variables is just the opposite.

There is considerable inconsistency in yearly fluctuations of population size among the various species (Figs. 32-34). Special attention was given to *B. leucopterus.* Counts of chinch bugs hibernating in the litter and ground were made in the middle of the winter at three locations on the south side of Brownfield Woods. An average of these counts, shown in Fig. 34, verifies the small peak observed in William Trelease Woods in 1953-54 and perhaps again in 1965. The large peak of 1933-36 occurred generally over central Illinois (Shelford and Flint, 1943).

Special mention may also be made of the cydnid *Allocoris pulicaria* (Germ.). The species was found regularly at William Trelease Woods in the early 1920s by Weese (1924), and there was an irruption in 1935 and 1936 with monthly maxima of 145 and 82 individuals. None was found from 1939 through 1943 and only a few thereafter until counts of this species were discontinued in 1967.

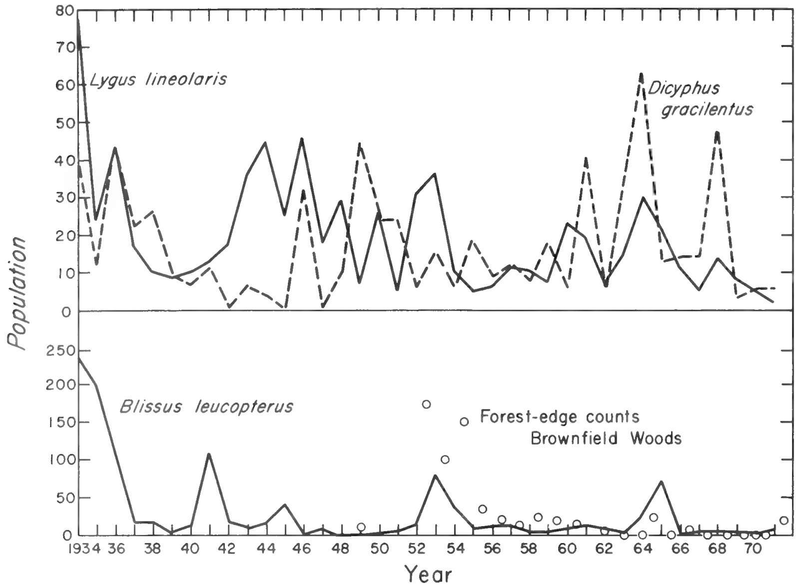

Fig. 34. Yearly fluctuations in maximum monthly populations of hemipterans.

Every independent variable enters into at least one predictive equation (Appendix). The population size the preceding year (PP) and ultraviolet radiation (U_1, U_2), both positive, occur most frequently. Also occurring conspicuously are the temperature during May of the preceding year (T_7, T_{10}), June temperature (T_2, T_5), and April-May precipitation (P_1, P_{10}), the latter two for the current year. The general response to both temperature and precipitation seems to be positive.

Homoptera (Leafhoppers, Others)

Although homopterans are abundant in the woods, only one species was followed in detail. The leafhopper *Osbornellus auronitens* has a symmetrical year curve of abundance with a peak in August (Fig. 35). An August peak also occurs in the data for Brownfield Woods and Funk Forest. This type of curve may be typical for other species of leafhoppers but with the peak coming at different times. Homopterans as a whole are most numerous in September and October. Although neither adults nor nymphs of *O. auronitens* were found

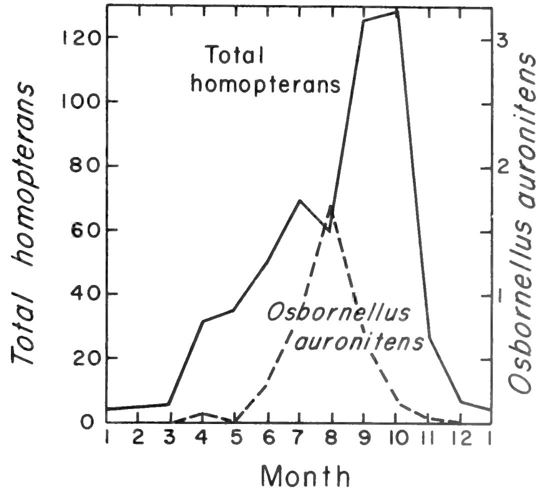

Fig. 35. Mean monthly populations of homopterans.

during the winter months, individuals of other species were recorded. Leafhopper species overwinter either in the egg, nymph, or adult stage, and they vary in having 1, 2, or sometimes 3 generations per year.

Populations of *O. auronitens* were low in 1941-42, high between 1945 and 1948, low again from 1957 to 1959, and higher thereafter. All homopterans had low populations in 1957-58 (Fig. 36). The size of the population the previous year (PP) is included in all the predictive equations (Appendix).

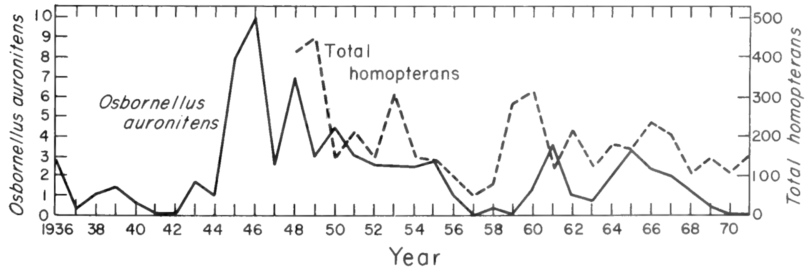

Fig. 36. Yearly fluctuations in maximum monthly populations of homopterans.

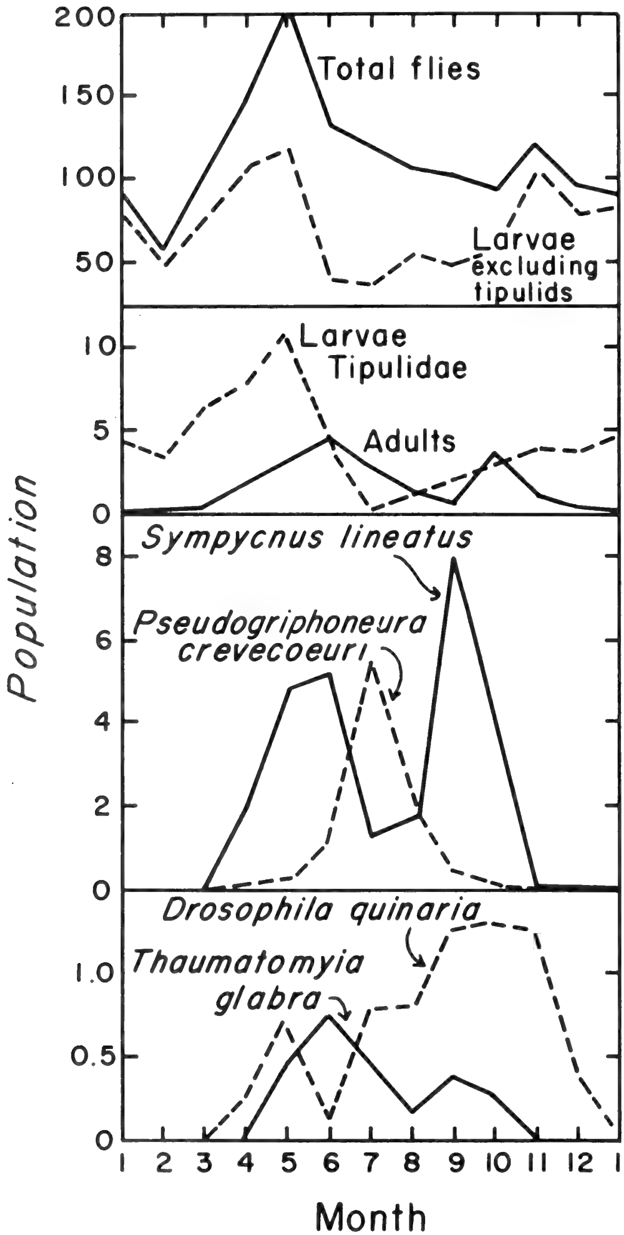

Fig. 37. Mean monthly populations of flies.

Diptera (Flies)

A large variety of flies occurs in the woods; Weese (1924) listed 68 species. We followed only 5 species throughout. Flies as a whole, including both adults and larvae, are most numerous in May, but different species reach peak populations in May, June, July, and September-November, which suggests some sort of interspecies adjustment for dividing the natural resources on a time schedule (Fig. 37). The two peaks for *Sympycnus lineatus* in May-June and September, with lows in July-August, are fully supported by the data for Brownfield Woods and Funk Forest, likewise the single peak in July for *Pseudogriphoneura crevecoeuri* and the highest populations of *Drosophila quinaria* during the autumn months. Flies may overwinter as eggs, larvae, pupae, or adults, although few adults were found in our collections during the winter months. Some species have several generations during the warm months.

Highest populations of several species came during the mid- and late forties with scattered peaks at other times (Figs. 38, 39). The size

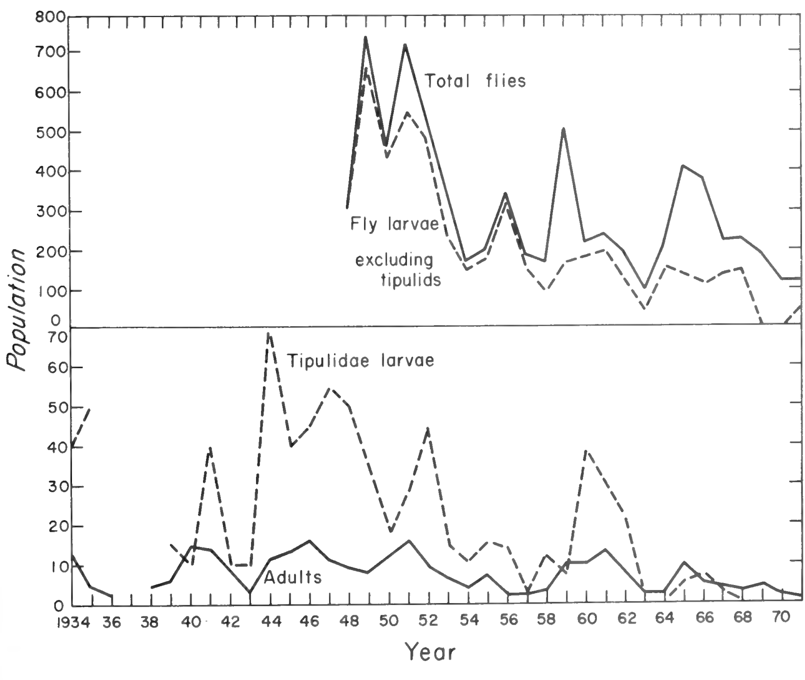

Fig. 38. Yearly fluctuations in maximum monthly populations of flies.

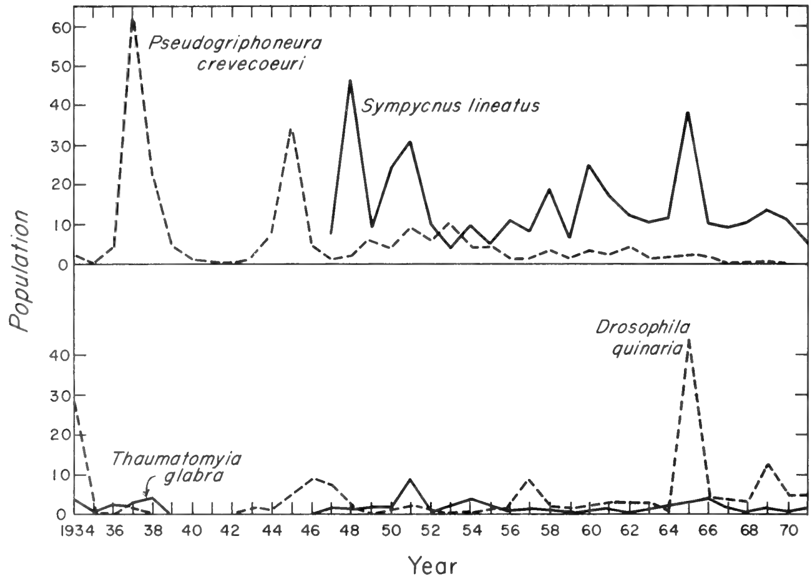

Fig. 39. Yearly fluctuations in maximum monthly populations of flies.

of the population the preceding year (PP) enters into nearly all the predictive equations (Appendix). Next most frequent is temperature the preceding winter (T_{13}) and total precipitation (P_5), both of which generally show a positive correlation.

Lepidoptera (Moths, Butterflies)

The lepidopterans are represented in the collections chiefly by larvae. They are present in fair numbers overwinter and from May through September (Fig. 40). The marked drop in numbers of larvae in William Trelease Woods during June may be significant since it also occurs in the populations at Brownfield Woods and Funk Forest. Perhaps at this time the spring larvae and pupae metamorphose into adults. Adults of *Dichomeris ligulella* reach their highest numbers in June, July, and August and were the only species regularly collected. Smith (1928) found *Graphium marcellus* (Cramer) and *Danaus plexippus* (Linnaeus). Adults do not overwinter in Illinois.

Four peaks in the population of total lepidopterans (larvae and adults) came at intervals of 5-6 years, and there was an outbreak of *D. ligulella* adults in 1938 (Fig. 41). In contrast with previous taxa

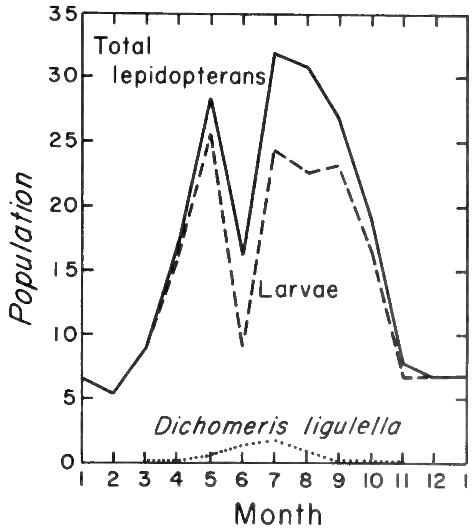

Fig. 40. Mean monthly populations of lepidopterans.

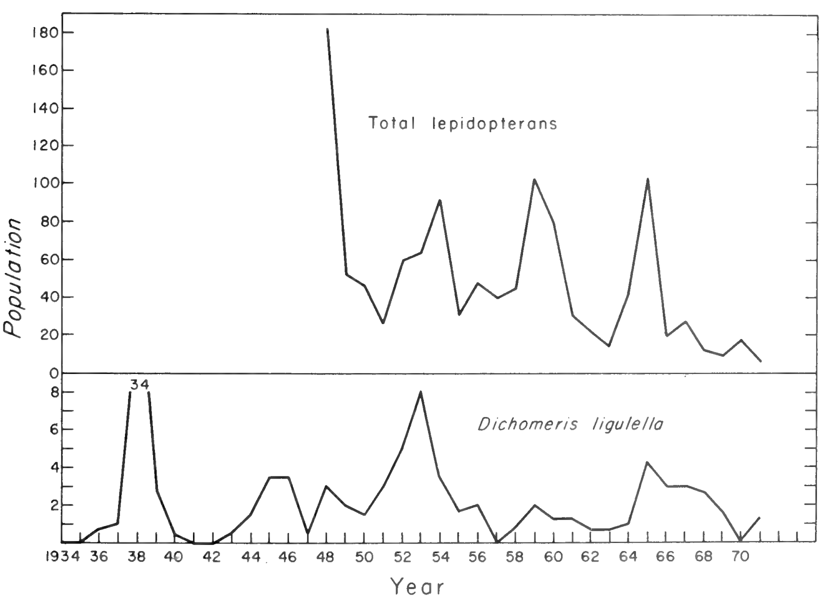

Fig. 41. Yearly fluctuations in maximum monthly populations of lepidopterans.

considered, the size of the population the previous year (PP) enters into the predictive equations only once (Appendix). The most frequent variable is the minimum temperature the preceding winter (T13), always showing a positive correlation. Most of the precipitation variables indicate a negative correlation.

Coleoptera (Beetles)

Beetles are the most abundant and diversified group under consideration; Weese (1924) listed 112 species in William Trelease Woods. They make up around 36 per cent of the total woods population, of which the rove beetles, Staphylinidae, are most numerous.

Beetles commonly overwinter as adults and also in immature stages. The two peaks evident in the populations of most forest species (Fig. 42) in all three woods are probably explained by the overwintering

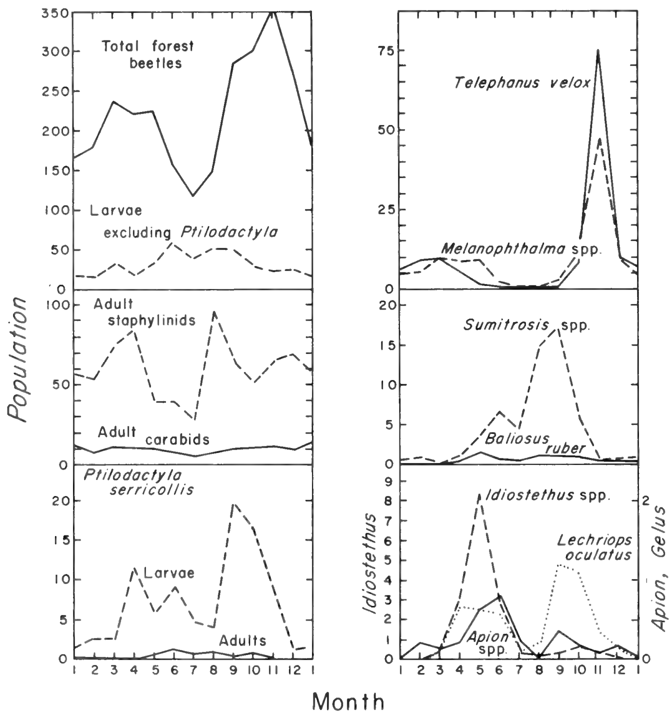

Fig. 42. Mean monthly populations of beetles.

adults maturing and ovipositing in the spring, then dying, and by new adults emerging in the autumn. Adult carabids do not show the two peaks. In this group the overwintering adults begin to oviposit in March, April, or May, require a year to develop into adults, and may live 2, 3, 4, or more years (Balduf, 1935). In William Trelease Woods spring populations of *Telephanus velox* and *Melanophthalma* spp. are lower than autumn populations, but in Brownfield Woods and Funk Forest the two peaks are about equal. Weese (1924) thought that *T. velox* migrated out of the woods in the summer, which would explain their near absence from the collections from May through September, but it may be that the overwintering adults simply die quickly after ovipositing early in the spring and the next generation does not mature until late in the autumn. According to Shelford (1951a), adults of *Sumitrosis inaequalis* emerge from hibernation about May 1, and the minor peak in June is probaby composed of these individuals. The new generation begins to appear in early July, as the older generation dies, and makes up the August-September peak. *Idiostethus* has high spring and low autumn populations in all three areas.

Four species of beetles, *Notoxus, Acalymma vittata, Diabrotica undecimpunctata,* and *Cerotoma trifurcata,* as well as the two species of hemipterans discussed earlier, *Lygus lineolaris* and *Blissus leucopterus,* overwinter in the forest but largely leave the forest during the summer (Figs. 31, 43), when they become important pests on farm and garden crops. Hibernation sites of these species are most prevalent within 30 m of the forest edge, especially on the sunny south side, but occur sparingly through most of the forest interior (Kennedy, 1958). The bean leaf beetle, *C. trifurcata,* is of special interest (Fig. 43). The decrease in its numbers in the woods in May agrees with the time they are first observed in the soybean fields. Here their first generation matures in July and early August, oviposits, and then dies. The second generation becomes adult in September (Waldbauer and Kogan, 1976). Some individuals reappear in the woods almost immediately, but the overwintering population along the border of the forest does not reach its maximum until January.

Populations of most forest species were relatively high during the mid- or late 1940s, and some species showed a resurgence again in the mid-1960s (Figs. 44-47). Nonforest beetle and hemipteran populations were largest in the mid-1930s (Fig. 47), but individual species have peaked during different years (Figs. 34, 45-46). The bean leaf beetle occurred in William Trelease Woods in the early 1920s (Weese,

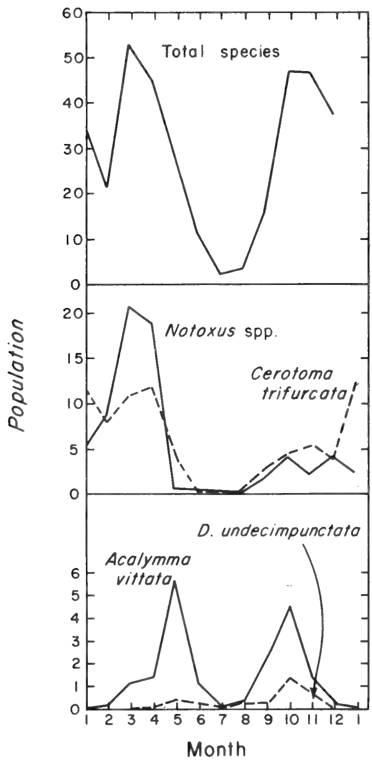

Fig. 43. Mean monthly populations of nonforest species.

1924) and in small numbers in our early collections but not commonly enough to attract special attention until populations began to be measured in 1953. Perhaps the increase in its numbers is correlated with the expansion of soybean farming in central Illinois. Kogan et al. (1974) noted extensive damage to soybean crops in Illinois in 1953, 1955, 1959, 1964, and 1966.

Every independent variable is included at least twice in the 62 predictive equations (Appendix). The most frequent variables are the population size the preceding year (PP) 20 times, ultraviolet intensity (U_1) 18 times, and May temperature (T_7) and April-May precipitation (P_6), both for the preceding year, 11 times each. The correlations with temperature (T_7, T_{10}) were generally positive but with precipitation and ultraviolet radiation about equally positive and negative. The population sizes of nonforest species were probably also affected by exposure to insecticides and other means of control in recent years, but this cannot be quantified.

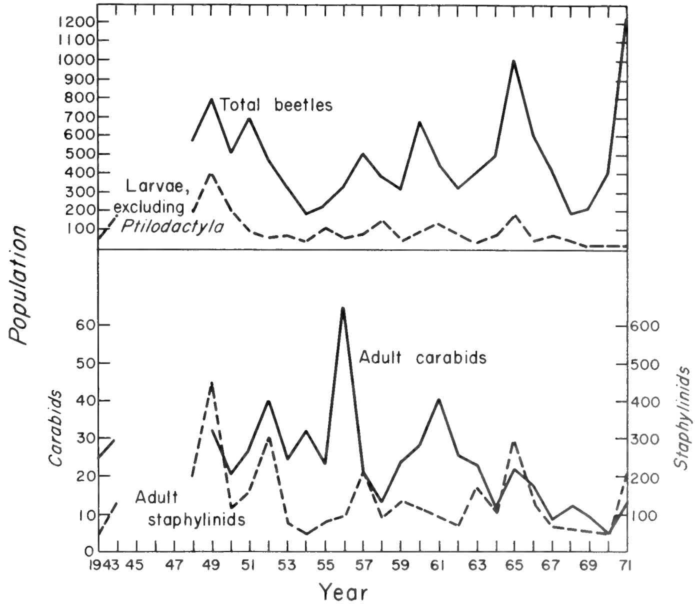

Fig. 44. Yearly fluctuations in maximum monthly populations of beetles.

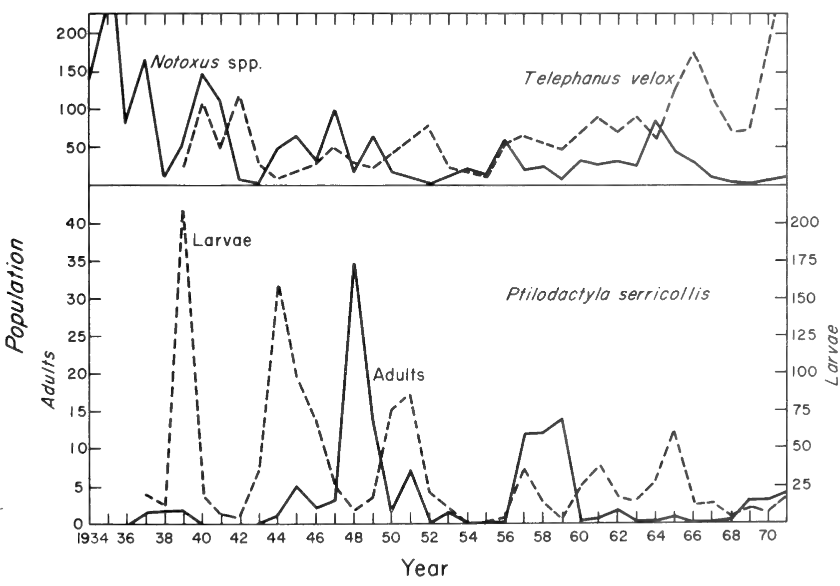

Fig. 45. Yearly fluctuations in maximum monthly populations of beetles.

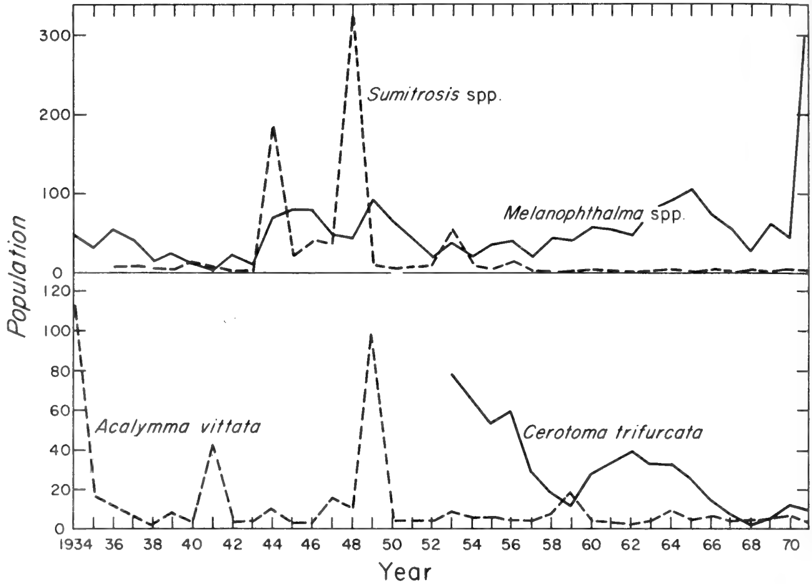

Fig. 46. Yearly fluctuations in maximum monthly populations of beetles.

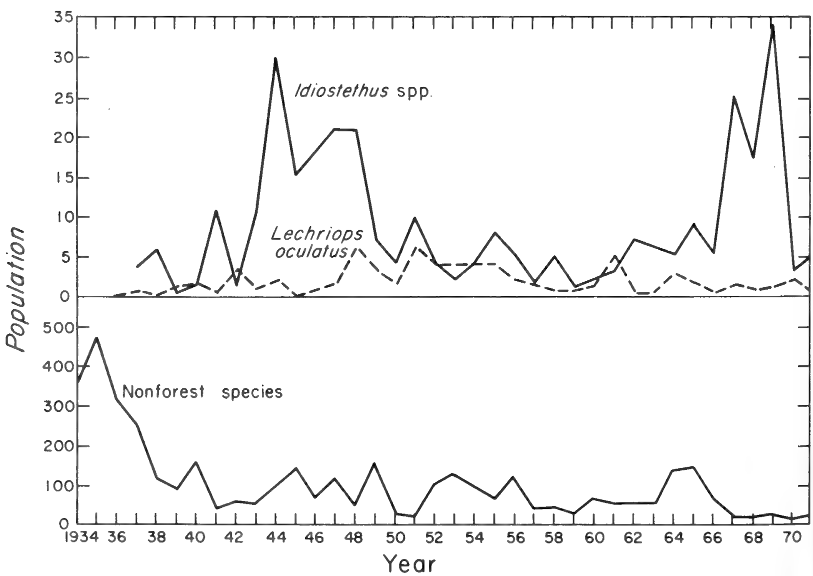

Fig. 47. Yearly fluctuations in maximum monthly populations of beetles.

Formicidae (Ants)

Most of the Hymenoptera sampled were ants, although Weese (1924) recorded 19 species of Braconidae, Chalicidae, and Ichneumonidae in the herbs and shrubs of William Trelease Woods. For the years 1967 through 1971, mean monthly populations of hymenopterans were measured and varied from 2.0 in February to 22.2 in June.

Ground and litter ants are present throughout the year, although larger numbers were collected between April and October. The peaks in May-June and September may represent different generations (Fig. 48). Many individuals during the winter may have gone deeper into the ground and avoided capture. During the summer ants of several species wander freely between the ground and the herbs and shrubs. In the latter strata they are most numerous in mid-summer.

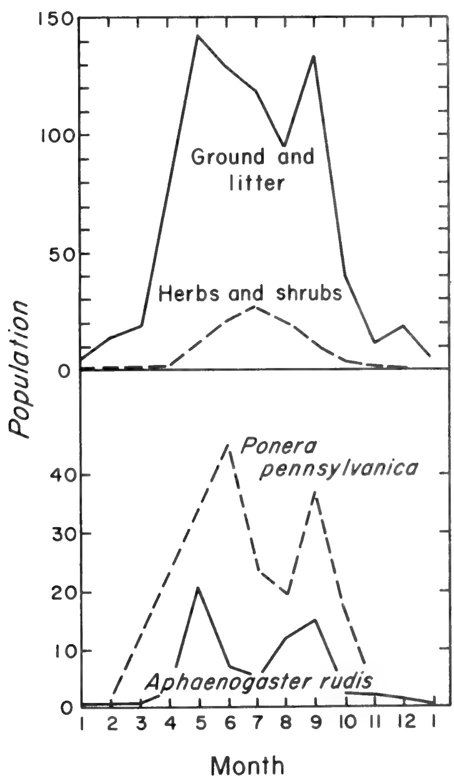

Fig. 48. Mean monthly populations of ants.

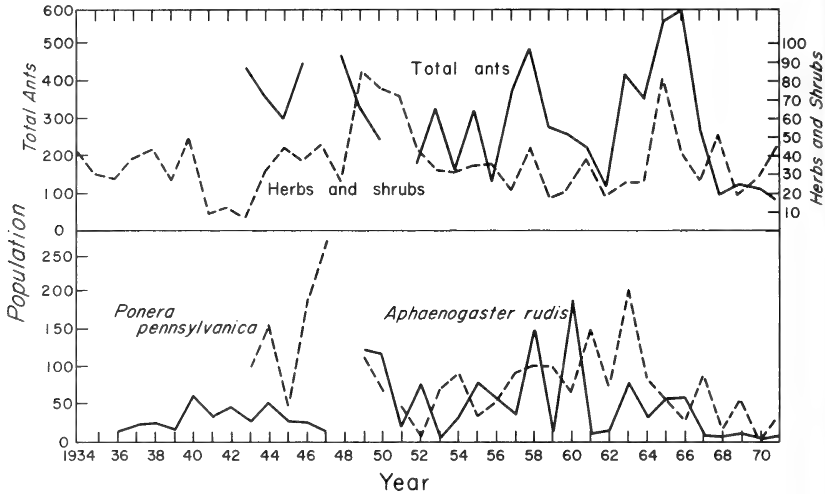

Fig. 49. Yearly fluctuations in maximum monthly populations of ants.

Besides the 2 species included in this study and 12 other species recorded by earlier investigators for the William Trelease Woods, W. L. Brown, Jr., and L. J. Stannard found *Leptothorax schaumi* Roger, *Camponotus nearcticus* Emery, and *Lasius alienus* (Foerster) on August 8, 1958.

Populations appear to have been high in the late 1940s and again in the late 1950s and early 1960s (Fig. 49). The population size the preceding year (PP) is the most frequent variable (6 times) in the predictive equations (Appendix), although 8 different temperature variables occur 14 times and 7 different precipitation variables 13 times. Plus or minus correlations with temperature lack consistency, but most correlations with precipitation are positive.

Mollusca (Snails, Slugs)

Twenty-seven species of snails and slugs have been collected in William Trelease Woods (Table 8). Several of these species were not common enough to census regularly. Some species are grouped for analysis because of difficulty in quick separate identifications. Immature forms are combined with adults in the counts.

In the large snail *Mesodon thyroidus* fertilization may take place in the autumn and eggs deposited beginning early in the following spring. Hatching extends over several months; the young overwinter

Table 8. Species of Mollusca (snails, slugs) recorded at William Trelease Woods by Weese (1924), Blake (1926, 1931), Smith (1928), and in this study. Nomenclature and sequence of listing follow Pilsbry (1939-48)

Mesodon thyroidus (Say)[1,2]	*Punctum minutissimum* (Lea)[1]
Mesodon pennsylvanicus (Green)[1]	*Philomycus carolinianus* (Bosc)[2]
Triodopsis albolabris (Say)[2]	*Pallifera dorsalis* (Binney)[1]
Haplotrema concavum (Say)[1]	*Succinea avara* (Say)[2]
Euconulus sp.[1]	*Gastrocopta contracta* (Say)[1]
Retinella electrina (Gould)[1]	*Gastrocopta pentodon* (Say)[1,2]
Retinella indentata (Say)[1,3]	*Gastrocopta tappaniana* (Adams)[2]
Paravitrea sp.[1]	*Vertigo milium* (Gould)[2]
Hawaiia minuscula (Binney)[2,3]	*Vertigo ventricosa* (Morse)[3]
Zonotoides arboreus (Say)[2]	*Vertigo tridentata* Wolf[1,3]
Striatura milium (Morse)[2]	*Columella edentula* (Draparnaud)[1,3]
Deroceras reticulatum (Müller)[3]	*Carychium exiguum* (Say)[2]
Deroceras laeve (Müller)[3]	*Carychium exile* (Lea)[1]
Anguispira alternata (Say)[1]	

[1] Identifications confirmed by G. R. Webb.
[2] Identifications confirmed by F. C. Baker.
[3] Identifications confirmed by H. Van der Schalie.

and do not attain full growth and sexual maturity until the autumn of the following year. The usual length of life seems to be 3 or possibly 4 years (Van Cleave and Foster, 1937).

The life cycle of the smaller snail *Succinea ovalis* consists of birth in the spring, growth to maturity by late summer, hibernation overwinter, reproduction the following spring, and death by June (Strandine, 1941). The life cycle of other small snails may be similar, as they overwinter in adult form (Blake, 1926).

The slug *Deroceras reticulatum* has its chief egg-laying period in the northeastern United States in late summer and autumn. The eggs hatch in three or four weeks, and the newly hatched young are chiefly the forms that overwinter. Sexual maturity is attained late the following summer, and the adults die soon after the eggs are laid. In southern localities there may be 2 generations per year with the spring hatch maturing in the autumn and the autumn hatch in the following spring (Chichester and Getz, 1973).

Snails in William Trelease Woods generally reach maximum populations in September, but the slug *Deroceras* is most numerous during early summer, and the predaceous snail *Haplotrema concavum* maintains a stable population throughout the year (Fig. 50). In Brownfield Woods high populations are maintained from June through September with the peak coming in July; in Funk Forest the peak comes in September, although it is not much higher than the one in July.

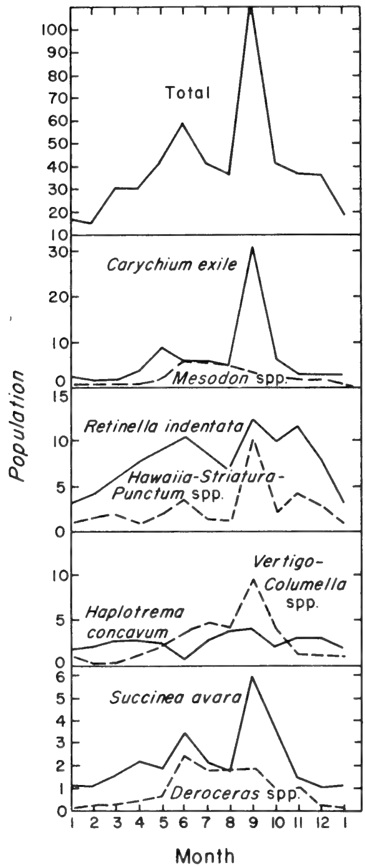

Fig. 50. Mean monthly populations of snails and slugs.

In northern Illinois *S. ovalis* reaches a peak in June, decreases in numbers to August, and increases again somewhat in September (Strandine, 1941). This is similar to the pattern for *S. avara* (Fig. 50) in east-central Illinois except that the September peak is higher than the one in June. The low numbers in August in this and other species may be due to the snails going in and under logs or burying themselves deeper into the soil as a response to high temperatures combined with decreased precipitation.

In the yearly fluctuations peak numbers for snails and slugs occurred in 1937-38, between 1948 and 1952, and in 1960 (Figs. 51, 52). It is of interest that while the first two peaks also occurred with

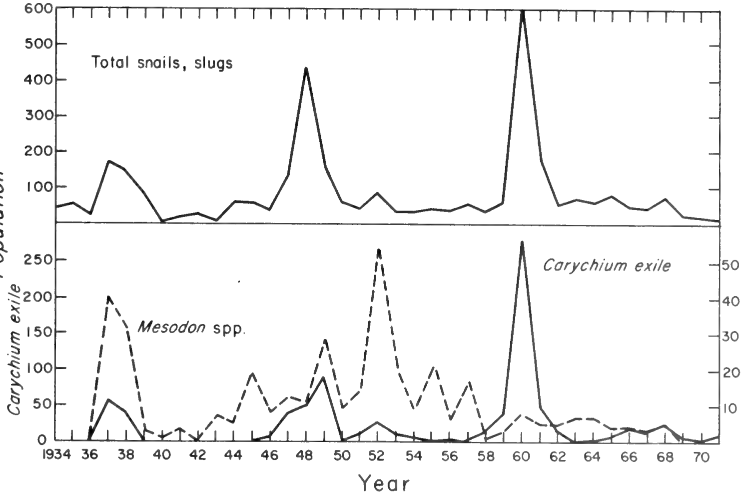

Fig. 51. Yearly fluctuations in maximum monthly populations of snails and slugs.

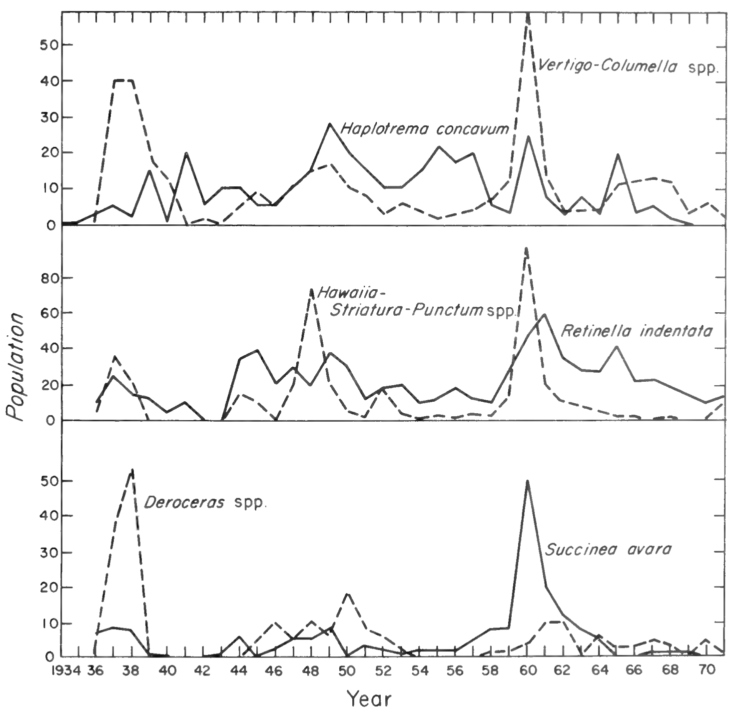

Fig. 52. Yearly fluctuations in maximum monthly populations of snails and slugs.

populations of the ground-inhabiting millipedes and centipedes, the 1960 peak did not. The predictive equations (Appendix) indicate that population size is positively correlated with the size of the population the preceding year (PP) and temperature (T_{13}) and snowfall (S_1, S_2) the preceding winter.

9. Discussion

The Yearly Cycle

All adult populations of the forest species considered decrease in size during the autumn and winter, owing to die-off, and increase again during the following spring and summer, owing to reproduction. Adults or semi-adults of many species overwinter, but some species overwinter chiefly as eggs, larvae, or pupae. The time of beginning and end of the winter quiescent state varies, apparently depending on how the species responds to decreasing photoperiod and temperature in the autumn and increasing photoperiod and temperature in the spring, especially in relation to its diapause period (Tauber and Tauber, 1976). Moisture conditions and food supplies are doubtless also involved.

A single major peak of numbers during the warm months indicates a single generation or reproductive period per year. The life cycle of these species commonly spans a year but, in some cases, two or more years. Where there are two peaks, it usually means that the overwintering population has reproduced in the spring and then died, with a second generation maturing by late summer or autumn. This is not true, however, with nonforest species that leave the woods during the summer to feed and reproduce on surrounding farm crops, nor is it true where forest species escape collection because of aestivation during warm dry weather. The height of the peaks gives a rough index of the extent of reproduction and, along with the length of time that high populations are maintained, the impact of the species in the forest community.

An "Island" Fauna?

William Trelease and Brownfield Woods and, to a lesser extent, Funk Forest are "islands" in a "sea" of farmlands. Island faunas have

been shown by MacArthur and Wilson (1967) to be in a more or less continuous flux as new species invade and ones already on the island disappear. It is possible, as Weese (1924) stated, that with clearing of the land surrounding these wooded areas for agricultural purposes, some truly forest species have disappeared and been unable to return. Certainly some other species, particularly those that utilize agricultural crops, have greatly increased in numbers where formerly they were rare or absent. In this study we have noted a few changes in forest species composition over the years, particularly among millipedes, spiders, and hemipterans. However, the absence of a species in our collections does not necessarily mean it is not present in small numbers elsewhere in the woods. These invertebrate populations are subject to wide fluctuations in numbers, and we have no evidence that sufficient numbers are not present at all times to maintain a continuous breeding population ready to explode whenever favorable conditions reoccur. It may well be that while these wooded areas may be small enough to constitute "islands" for the large vertebrate species, they are essentially "continents" for the much smaller invertebrates.

Yearly Fluctuations

The structure of the forest community, as defined by the densities of the constituent species, is certainly not fixed, and the invertebrate populations cannot be said to be stabilized except within wide limits. A short time study restricted to part of a year or to a few years will not provide an adequate approximation of the long-term situation.

Irruptions in population size extending over a 10-year period from the mid-1940s to the mid-1950s were conspicuous in many taxa. Different taxa attained peaks during different years in this period, and the peaks seldom lasted longer than a few years. Irruptions involving fewer species also occurred in the 1960s. These surges in abundance cannot be related to the extensive destruction of elm trees beginning in the 1950s, nor can they be related to any conspicuous change in weather. However, each species responds to weather fluctuations in its own way. It may be coincidence that several species found weather conditions especially favorable during the most sensitive periods of their life cycles in these particular years. The life cycles of many of these invertebrates are short and reproductive rates are high, so that populations are potentially explosive whenever favorable conditions occur.

A fairly large number of graduate students were involved in collecting the field data, but I have been unable to detect any important aberrations in the counts that could be ascribed to differences in skill or care with which they did their work. Many worked for two consecutive years, a few for three or more years, but some for only a few months. The same person was always responsible for the collections in all three wooded areas.

The Predictive Equations

The total number of significant equations obtained for the three woods varied almost exactly in the ratio of the number of year's record for each or approximately in the ratio of William Trelease Woods, 2.3, to Brownfield Woods, 1.3, to Funk Forest, 1.0. The longer the period of record, the more opportunities were provided for the effect of different factors to be expressed.

Among the equations there were more that included only one environmental variable than included more than one; in fact, there were over twice as many equations that included only one or two variables than the combined total of all the others (Table 9). The total number of significant correlations was approximately the same for the total yearly indices as for the maximum monthly populations.

The lowest significant multiple correlation coefficient (R) obtained was 0.33, the highest 0.999. The coefficient generally increased with the number of significant variables included in the equation, although there was considerable overlap in values so that differences between at least adjacent coefficients are not significant. There was a tendency for maximum monthly populations to have lower coefficients than total yearly indices. The coefficients increased in size from William Trelease Woods to Brownfield Woods to Funk Forest which is correlated with a decrease in the number of years' data for the three woods.

For several species no significant correlation between yearly fluctuations in population size and any of the independent variables was found. The number of variables included in the equations for other species varied greatly, with the largest number (10) obtained with the stepwise procedure for the total yearly index of the dipteran *Sympycnus lineatus* in Brownfield Woods. The backward elimination procedure provided generally a larger number of variables than the stepwise multiple regression — up to 25 for the maximum monthly populations of the lepidopteran *Dichomeris ligulella.*

Table 9. Distribution of variables and mean multiple correlation coefficients in the equations obtained by the stepwise regression procedure in the three woods

Number of Variables Included	Total Yearly Indices							
	Trelease		Brownfield		Funk		Total	
	No.	Mean	No.	Mean	No.	Mean	No.	Mean
1	21	0.53	24	0.59	21	0.58	66	0.57
2	24	0.68	17	0.76	17	0.78	58	0.73
3	12	0.74	6	0.83	3	0.88	21	0.79
4	4	0.86	5	0.87	4	0.93	13	0.89
5	3	0.80	3	0.88	1	0.95	7	0.86
6	1	0.92			1	0.98	2	0.95
7			2	0.96			2	0.96
8								
9								
10			1	0.993			1	0.993
Total	65	—	58	—	47	—	170	—

Considering only the weather factors, 43 per cent of the partial regression coefficients showed that the variables affected both the yearly index and the maximum monthly population in the same species. Of these variables, there is agreement that their coefficients are either both positive or both negative in 98 per cent of the cases. The other 57 per cent of the coefficients were associated with variables affecting either the yearly index or the maximum monthly population, but not both.

Of the total number of times that weather variables entered into the equations for the three woods, only 17 per cent occurred in equations for two or all three woods in individual taxa. Of these, 77 per cent agreed in being either positive or negative. In other words, 83 per cent of the variables applied to only one of the areas, and different variables for a taxon occurred in the equations for the other two areas. One would expect that if a particular weather factor was a good indicator of population size in one woods, it would also be good in other nearby areas, except as it may be affected by differences between the areas in vegetation, terrain, soil, or other organisms. The equations for William Trelease Woods, calculated from a longer series of data over the years, are the most thoroughly tested and should be the most reliable.

Table 9 (Continued)

Maximum Monthly Populations								Grand	
Trelease		Brownfield		Funk		Total		Total	
No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean
24	0.48	15	0.51	20	0.61	59	0.53	125	0.55
18	0.66	20	0.70	12	0.75	50	0.70	108	0.72
15	0.72	8	0.79	8	0.84	31	0.77	52	0.78
3	0.78	3	0.89	4	0.93	10	0.87	23	0.88
1	0.74	3	0.91			4	0.87	11	0.86
1	0.81	2	0.93	2	0.98	5	0.93	7	0.93
		2	0.97	1	0.99	3	0.98	5	0.97
				1	0.999	1	0.999	1	0.999
				1	0.999	1	0.999	1	0.999
								1	0.993
62	—	53	—	49	—	164	—	334	—

Weather Factors

The frequency with which a variable entered into the predictive equations may be, to some degree, an index to its relative importance in determining population size. Table 10 gives a ranking of the variables in all the predictive equations, including many with lower *R* values not listed in this monograph. Most important are the size of the population the preceding year (PP) and the number that survive overwinter dependent on temperature (T_{13}). The regression coefficients for these variables are, with one or two exceptions, positive. The dependence on the population size the preceding year is evident in the analysis of each taxonomic group except for harvestmen, woodlice, and lepidopterans. The number of equations for the first two groups is small, while for the lepidopterans survival overwinter (T_{13}) assumes major importance.

The high ranking of ultraviolet intensity, especially from April through July of the current year (U_1), supports the findings of Shelford (1951a, b). More experimental work should be directed toward this variable. Correlations are sometimes positive, sometimes negative. The present analysis does not show whether ultraviolet radiation is effective by direct action on the organism or indirectly through the food eaten or some other aspect of the environment. It may be

Table 10. Number of times each variable entered into all predictive equations for all three woods, arranged in descending order of combined frequency for A_y and A_m

	A_y	A_m		A_y	A_m
PP	86	67	T_{12}	9	8
T_{13}	29	22	P_9	4	13
U_1	23	25	T_{10}	9	7
P_6	16	17	TP_2	5	11
P_3	13	16	TP_3	7	8
P_5	17	12	T_6	7	7
T_7	11	15	S_2	8	5
P_7	11	14	T_8	3	9
P_{11}	11	12	T_{11}	6	5
U_2	13	9	T_4	5	5
P_8	12	9	P_{10}	4	6
P_4	8	12	T_1	4	5
TP_1	10	10	P_2	4	5
S_1	10	9	T_2	3	5
T_3	6	11	T_5	3	5
T_9	8	9	P_1	3	4

that the ultraviolet units used simply reflect fluctuations in the total solar radiation and that this may be related to temperature and precipitation. Fluctuations in ultraviolet intensity have at least some usefulness as a predictive factor.

Precipitation variables occur considerably more frequently in the equations than do variables concerned with temperature. This again agrees with Shelford's (1951a, b) contention that fluctuations in rainfall affect the size of invertebrate populations more than do fluctuations in temperature, particularly during the reproductive period. Rainfall may affect the animals directly, especially when it is high, or indirectly through the vegetation and food supply. It is sometimes difficult to find consistency in the manner in which precipitation variables influence population size, but in most cases the correlations are positive. Apparent exceptions are centipedes and lepidopterous larvae. The correlations may vary not only between species but also with the time of year. The relationship of any one variable may also vary because of the simultaneous influence of some other factor; for instance, rainfall may be unfavorable at a low temperature and favorable at a high temperature, or vice versa. Finally, the plus or minus sign of a variable may depend on the step at which it enters into the computer computations.

It is of interest that 3 of the first 4 most frequent variables in the predictive equations are concerned with populations and weather conditions the preceding winter or year, in agreement with what Uvarov (1931) stated was necessary for successful forecasting.

Other Factors

The multiple correlation coefficient (R), when squared, becomes the coefficient of determination (R^2) (Zar, 1974), which represents the proportion of the fluctuations in population size that is accounted for by the weather factors and the population size the preceding year. If the population fluctuations were completely explained by the given variables, R^2 would be 1.00. The difference $(1 - R^2)$ represents the proportion of the variability in population size not accounted for, i.e., that portion or percentage of the variability due to factors other than the listed ones.

"Other factors" could be expected to include such biological ones as predation, parasitism, disease, competition, fecundity, and food supply, as well as "noise." "Noise" may result partly from inaccurate measurements of population size; the minor fluctuations from year to year may represent only deficiencies in population sampling. Furthermore, macroclimatic data have been used of necessity in the analysis, yet each species is exposed to a microclimate that may vary from year to year at a different rate and manner than the macroclimate.

A few species show a very high R value in the predictive equations (Table 9) with R^2 values of nearly 1.00. However, when averages are made for the different taxonomic groups, all R^2 values fall between 0.43 for ants and 0.59 for flies, except centipedes where R^2 is 0.77. This leaves the proportion of the fluctuations unaccounted for at 57, 41, and 23 per cent respectively, which is quite large.

A part of this unaccounted-for fraction results from reducing the number of variables in the predictive equations (Table 6). Therefore, to estimate the importance of "other factors," use was made of the first run of the backward elimination procedure where all the variables are included, even those which individually may have little statistical significance. Table 11 shows that two-thirds of the values are less than 10 per cent and two-fifths are less than 5 per cent. For these taxa fluctuations in population size are largely accounted for by the fluctuations in weather and population size the preceding year. There are several taxa, however, where the unaccounted-for

Table 11. The relative importance ($1 - R^2$) of "other factors" in accounting for population fluctuations, expressed in percentages

Taxon	A_y	A_m
Total woods: herbs and shrubs	16.5	36.6
ground	5.5	7.1
Woodlouse, *Tracheoniscus rathkei*	25.0	14.8
Centipedes, Chilopoda	5.1	7.6
Tree cricket, *Oecanthus angustipennis*	3.8	2.2
Hemipterans, *Zelus exsanguis*	1.8	1.4
Gargaphia tiliae	20.8	13.7
Corythuca aesculi	1.2	0.4
Lygus lineolaris	2.8	0.8
Horcias dislocatus	8.0	14.6
Dicyphus gracilentus	0.8	1.6
Blissus leucopterus	1.8	6.1
Jalysus spinosus	6.9	8.8
Leafhopper, *Osbornellus auronitens*	4.2	3.0
Flies, Tipulidae, adults	3.2	1.0
larvae	20.4	38.5
Pseudogriphoneura crevecoeuri	0.8	1.0
Thaumatomyia glabra	9.4	5.1
Drosophila quinaria	10.1	9.8
Moth, *Dichomeris ligulella*	4.2	3.4
Beetles, *Notoxus* spp.	3.2	3.2
Ptilodactyla serricollis, adults	7.1	7.3
larvae	6.7	5.7
Telephanus velox	1.2	1.0
Melanophthalma spp.	11.1	8.4
Diabrotica undecimpunctata howardi	4.0	3.6
Acalymma vittata	7.3	9.9
Baliosus ruber	7.1	4.2
Sumitrosis spp.	21.7	14.8
Apion spp.	4.7	7.5
Idiostethus spp.	2.8	1.8
Lechriops oculatus	12.8	13.0
Ants, Formicidae, herbs and shrubs	4.2	0.8
Snails and slugs, *Carychium exile*	31.8	28.4
Mesodon spp.	6.1	9.2
Retinella indentata	10.1	12.4
Hawaiia, Striatura, Punctum spp.	29.4	31.9
Haplotrema concavum	12.6	13.3
Vertigo, Columella spp.	11.5	15.5
Succinea avara	20.3	26.6
Deroceras spp.	4.0	4.2

fraction is higher, the highest being tipulid fly larvae where it is 38.5 per cent. We do not know what portion unaccounted for may be "noise"; perhaps it is a large portion. The evidence indicates that the biological density-dependent factors listed above exert only a small role in determining population fluctuations between successive years. They may have a considerable role, however, in determining general equilibrium levels, although this was not investigated in the present study.

At this point I should caution the reader that one of my consultants with experience in the use of multiple regression procedures believes that linear regression models with more than 5 variables and an R^2 of over 0.85 are prone to produce spurious fits to the data owing to inherent statistical errors that are very difficult to avoid. About 10 per cent of the equations obtained by the stepwise regression procedure and a half-dozen or more from the backward elimination procedure that are given should therefore be viewed with some caution. The following section provides further background for evaluating the equations.

Prediction of Peak Populations

Equations possessing high multiple correlation coefficients (R) give predicted values each year that closely approximate observed population sizes (Fig. 53). When R is low, predicted values agree only with the general trends in the fluctuations and sometimes exhibit peaks or troughs in certain years when none existed. When an equation contains only a single weather variable, usually with a low R, the agreement is even less satisfactory (Fig. 54). A moderately good correlation with general trends may be obtained when the single included factor is the previous year's population size (Fig. 55), but predicted peaks and troughs often lag a year behind the observed ones.

Another test of the usefulness of the equations is how accurately they predict peak years. Peak years may have a special significance, since the species then has its greatest impact upon the ecosystem and for agricultural ecosystems may become of economic importance. Peak years were selected as those years when the population was at least 2-3 times the size of populations before and afterward, but not necessarily of the immediately adjacent years. These peak years were then matched with peaks in the predicted population size to determine if they came in the same year, the following year, the pre-

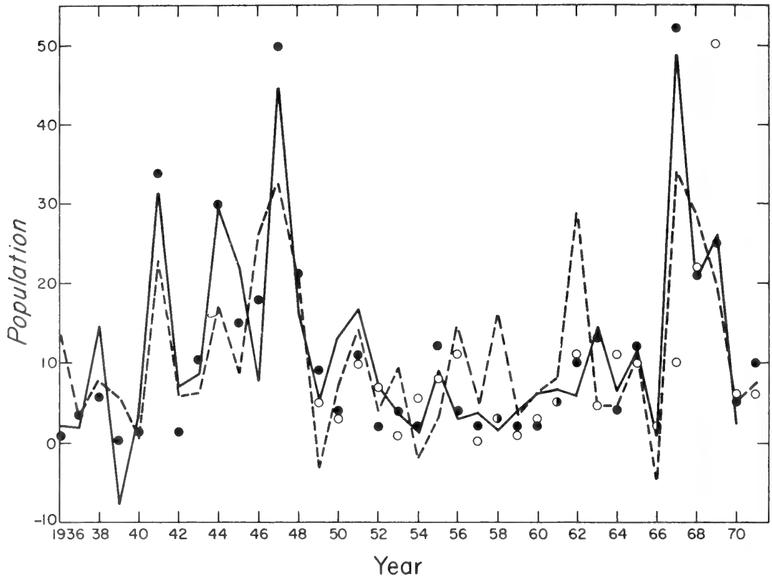

Fig. 53. Yearly fluctuations in maximum monthly populations of the beetle *Idiostethus tabulatus* in William Trelease Woods: actual measurements shown by solid dots, predicted values from equation obtained by backward elimination procedure involving 19 variables and $R = 0.94$ (solid line), and predicted values from equation obtained by stepwise procedure involving 4 variables and $R = 0.67$ (broken line). Brownfield Woods data shown by open circles. Funk Forest populations (not plotted) varied between 0 and 8 from 1955 through 1965, 13 in 1967, 5 in 1968, 26 in 1969, then down to 3 and 5 in 1970 and 1971.

ceding year, or were missed altogether. Since the sizes of the predicted populations do not fluctuate as much from year to year as do the measured populations, peak years in the predicted population were not necessarily 2-3 times the size of preceding and following populations. They were, however, usually larger than at least two of the immediately preceding and following years. Peak years in the measured and predicted populations were first compared for the William Trelease Woods. Then measured peaks for Brownfield Woods and Funk Forest were compared with peaks predicted for William Trelease Woods. This latter is a more rigorous test, since the peaks are based on different sets of data. When a peak in the predicted values came 2 or more years following or preceding the actual measured peak or when the predicted populations showed a progressive decline or increase, it was considered a "miss." Only

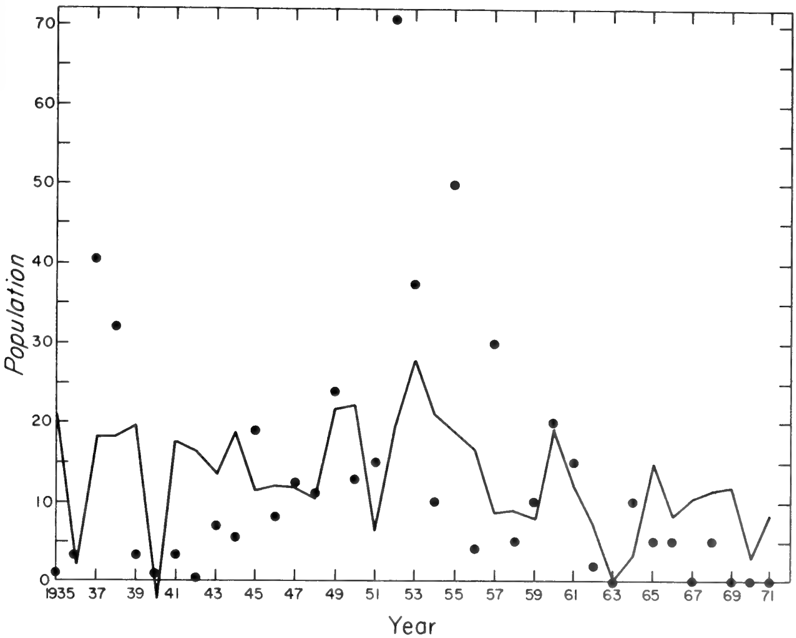

Fig. 54. Yearly fluctuations in the maximum monthly populations of the snail *Mesodon* in William Trelease Woods: actual measurements shown by solid dots, predicted values from equation obtained by stepwise procedure involving only the variable of mean minimum temperature of the preceding winter ($R = 0.44$).

the predictions based on equations from the stepwise multiple regression analysis were considered in this test. Separate tabulations were first worked out for the yearly total (A_y) and monthly maxima (A_m), but since they showed no significant differences in any of the three woods, they were combined in groups over ranges of 0.05 in R.

Although, as shown above, the multiple correlation coefficient (R) is a good index of the overall agreement between predicted and measured yearly populations, the coefficient has little or no value as an index of the amount of agreement between predicted and measured peak years (Table 12). Predicted peaks come as frequently during the same or immediately adjacent years with low R coefficients as with high ones. This was true for all three woods.

Combining all the data from each woods, the prediction of peak years within plus or minus 1 year was missed in only 8 per cent of the times in William Trelease Woods. The predictions were missed

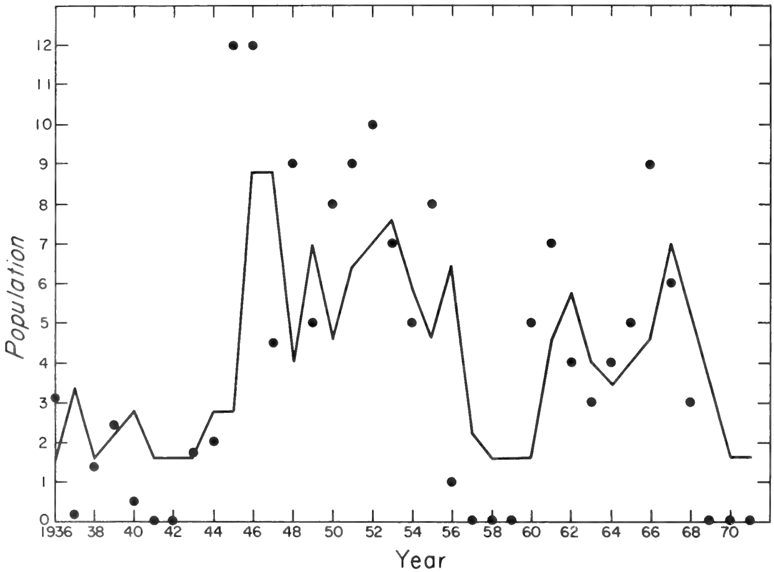

Fig. 55. Yearly fluctuations in the yearly index of the leafhopper *Osbornellus auronitens* in William Trelease Woods: actual measurements shown by solid dots, predicted values from equation obtained by stepwise procedure involving only the variable of the previous year's population size ($R = 0.60$).

about one-fifth of the times in the other 2 woods. The prediction of peak populations 1 year later or 1 year earlier than the measured peaks are almost as frequent as during the same year. High populations commonly extend over 2 or 3 years, so part of the inexactness may be explained by the difficulty in selecting the actual peak year in both the measured and predicted values when adjacent years have populations that differ by less than 2-3 times. The equations, therefore, have usefulness within these established limits.

Table 12. Accuracy in the prediction of peak years from equations obtained by stepwise multiple regression analysis of the William Trelease Woods data, combining data for yearly totals (A_y) and maximum monthly populations (A_m)

		Per Cent			
R	Number of Peaks	Same Year	One Year Later	One Year Earlier	Missed
		William Trelease Woods			
0.91-0.95	13	31	54	8	8
0.86-0.90	17	41	41	12	6
0.81-0.85	62	58	31	2	10
0.76-0.80	38	58	29	11	3
0.71-0.75	60	42	40	10	8
0.66-0.70	63	46	33	13	8
0.61-0.65	49	41	41	12	6
0.56-0.60	59	36	54	5	5
0.51-0.55	53	23	55	11	11
0.46-0.50	60	42	40	15	3
0.41-0.45	59	36	41	10	14
0.36-0.40	46	52	28	11	9
0.31-0.35	9	22	33	22	22
Total	588	42	40	10	8
		Brownfield Woods			
Total	306	34	25	21	20
		Funk Forest			
Total	209	37	25	15	22

10. Summary

The population sizes of arthropod and mollusk taxa were measured for 38 consecutive years in William Trelease Woods, 23 years in Brownfield Woods, and 17 years in Funk Forest, all located in east-central Illinois.

Each area is an isolated tract of about 24 ha (60 acres) surrounded by farmland, relatively undisturbed since primitive time, and dominated principally by sugar maple, red or white oaks, and basswood. There is a conspicuous seasonality in the leafing, flowering, and fruiting of both herbaceous and woody plants.

Six classes, 15 orders, 42 families, 49 genera, and 48 species of invertebrate animals are included in the study. Beetles, flies, spiders, spittle bugs and leafhoppers, and snails and slugs, in that order, were the predominant taxa.

Population sizes were measured weekly or biweekly, except monthly during the winter, by means of 48 sweeps each of herbs and shrubs and one-tenth m^2 samples of litter and soil. Fluctuations in population size of 200-300 per cent or more are considered statistically significant, and there is general agreement in monthly and yearly fluctuations between the wooded areas. Population factors analyzed are monthly means, maximum monthly, and yearly index, the last being the sum of the monthly means for the year.

Of 31 weather variables, 13 are concerned with temperature, 11 with precipitation, 3 with temperature times precipitation, 2 with snowfall, and 2 with ultraviolet radiation. In addition, the population size the preceding year is included as an independent variable as it represents the potential breeding population and may modify the correlations made with the weather factors.

There was a variation of about 48°F (27°C) in temperature, 5 hours in photoperiod, and 35 gcal cm^{-2} day^{-1} in ultraviolet intensity between winter and summer. Precipitation varied between approximately 2 inches (5 cm) in February to over 4 inches (10 cm) each in May and

June. Total snowfall during the year averaged about 15 inches (38 cm). All analyses are based on macroclimatic data, but differences between the macroclimate and the woods microclimate are indicated.

Animal inhabitants of the ground and litter maintained fluctuating populations within fairly uniform limits throughout the year. Herb and shrub populations were nearly absent during the winter but were high from May through October. Total combined populations reached peaks in September, and occasionally there was a smaller peak in May. Individual taxa, however, reached yearly peak populations during any month. Monthly populations were correlated with times of reproduction, number of generations per year, and longevity.

Many taxa reached peak yearly populations in the 10-year period between 1944 and 1953. Some taxa also peaked in the early and mid-1960s and at other times. Peak years occur during favorable weather conditions.

Multiple regression equations were obtained for each taxon for yearly fluctuations in population size as a function of 32 independent variables of weather and the previous year's population. Use was made of both the stepwise multiple regression and backward elimination procedures. These equations predicted population size with a high level of confidence when they included several variables and the multiple correlation coefficient was high.

The most frequent variables entering into these predictive equations were, in descending order, the size of the population the preceding year, mean minimum temperature the preceding winter, ultraviolet intensity from April through July, and rainfall during April and May the preceding year. Rainfall variables appeared more frequently in the equations than did variables concerned with temperature, suggesting their greater importance in determining population size.

High coefficients of determination (R^2) indicated that errors in measuring population size, noninclusion of pertinent microclimatic variables, and omission of such density-dependent biological factors as competition, predation, parasitism, fecundity, and disease were relatively unimportant in accounting for the fluctuations in population size.

Population irruptions were predicted (± 1 year) in 92, 80, and 78 per cent of the instances in William Trelease Woods, Brownfield Woods, and Funk Forest respectively.

The structure of the forest community, as defined by the densities

of the constituent species, is not fixed or stable. Individual species appear to be constantly present in at least small numbers and may irrupt at intervals of several years. They may form a conspicuous part of the community's species structure and exert a significant impact on the ecosystem only at times of such irruptions.

Appendix: Multiple Regression Equations

Multiple regression equations were obtained to predict size of yearly index (A_y) and maximum monthly population (A_m) using a variety of weather and other variables (for identification, see Table 2). All equations are based on data for William Trelease Woods except those marked (B) for Brownfield Woods or (F) for Funk Forest. The stepwise multiple regression procedure was used except for those equations marked (BEP), where the backward elimination procedure was employed. The standard error of the estimate is given as well as the multiple correlation coefficient (R).

TOTAL WOODS POPULATIONS

Grand Total

$A_y = 2326 + 0.69\ \mathrm{PP} \pm 2875$ $R = 0.69$
$A_m = 657 + 1.89\ \mathrm{TP}_2 \pm 622$ $R = 0.42$
$A_y(\mathrm{B}) = 2254 + 0.55\ \mathrm{PP} \pm 1107$ $R = 0.75$
$A_m(\mathrm{B}) = 368 + 33\ \mathrm{T}_{13} \pm 283$ $R = 0.48$
$A_m(\mathrm{F}) = -8122 + 112\ \mathrm{T}_7 + 1.05\ \mathrm{P}_5 + 0.14\ \mathrm{PP} \pm 388$ $R = 0.88$

Herbs and shrubs

$A_y = 674 + 0.63\ \mathrm{PP} \pm 552$ $R = 0.62$
$A_m = 204 + 0.12\ \mathrm{PP} \pm 166$ $R = 0.45$
$A_y(\mathrm{B}) = 1079 + 0.43\ \mathrm{PP} \pm 608$ $R = 0.46$
$A_y(\mathrm{F}) = 412 + 0.67\ \mathrm{PP} \pm 434$ $R = 0.66$
$A_m = 67 + 0.20\ \mathrm{PP} \pm 125$ $R = 0.67$

Ground

$A_y = 24574 - 312\ \mathrm{T}_3 + 0.82\ \mathrm{PP} \pm 1774$ $R = 0.86$
$A_m = 7893 - 92\ \mathrm{T}_3 - 66\ \mathrm{P}_7 + 0.11\ \mathrm{PP} \pm 455$ $R = 0.69$
$A_y(\mathrm{B}) = 1633 + 0.49\ \mathrm{PP} \pm 966$ $R = 0.68$
$A_m(\mathrm{F}) = -8077 + 109\ \mathrm{T}_7 + 1.45\ \mathrm{P}_5 - 1.51\ \mathrm{TP}_2 + 0.15\ \mathrm{PP} \pm 339$ $R = 0.92$

Opiliones (harvestmen)

$A_y = -64 + 2.6\ P_9 \pm 23$ $\quad R = 0.54$

$A_m = -30 - 2.2\ P_6 + 1.6\ P_9 \pm 7.5$ $\quad R = 0.71$

$A_y\ (F) = -5.7 + 3.2\ P_3 \pm 17$ $\quad R = 0.55$

$A_m\ (F) = -7.6 + 1.4\ P_6 + 0.23\ PP \pm 4.7$ $\quad R = 0.75$

Araneae (spiders)

Herbs and shrubs

$A_y = -26 + 0.07\ P_5 + 0.63\ PP \pm 73$ $\quad R = 0.73$

$A_m = 281 + 3.89\ T_8 + 3.08\ P_7 + 0.14\ PP \pm 18$ $\quad R = 0.71$

Mangora spp.

$A_y = -75 + 2.3\ P_9 + 0.63\ PP \pm 23$ $\quad R = 0.75$

$A_m = -97 + 0.01\ T_{11} + 1.3\ P_9 + 0.28\ PP \pm 12$ $\quad R = 0.74$

$A_y\ (B) = 164 - 2.4\ T_2 + 0.18\ P_{11} + 0.71\ PP \pm 9.5$ $\quad R = 0.92$

$A_m\ (B) = 60 - 0.87\ T_2 + 0.07\ P_{11} + 0.26\ PP \pm 4.1$ $\quad R = 0.90$

Hahniidae

$A_y = 146 - 0.70\ U_2 + 0.67\ PP \pm 17$ $\quad R = 0.69$

$A_m = -38 + 0.007\ T_6 + 0.22\ PP \pm 5.7$ $\quad R = 0.68$

$A_y\ (F) = -149 + 1.8\ T_9 + 0.014\ P_5 + 0.39\ PP \pm 5.1$ $\quad R = 0.87$

$A_m\ (B) = -7.2 + 0.59\ T_{13} + 0.09\ PP \pm 2.9$ $\quad R = 0.83$

Zygoballus spp.

$A_y = -2.8 + 1.11\ P_7 + 0.47\ PP \pm 8.2$ $\quad R = 0.59$

$A_m = 2.8 + 0.12\ PP \pm 2.9$ $\quad R = 0.38$

$A_y\ (F) = 0.28 + 0.78\ PP \pm 4.0$ $\quad R = 0.84$

$A_m\ (F) = 0.50 + 0.34\ PP \pm 1.3$ $\quad R = 0.90$

Isopoda (woodlice, sowbugs)

Tracheoniscus rathkei

$A_m = 80 - 4.9\ P_6 \pm 32$ $\quad R = 0.38$

$A_y(F) = 485 - 0.10\ T_6 + 0.20\ P_5 - 0.68\ P_{11} - 0.30\ TP_1 \pm 26$ $\quad R = 0.93$

$A_m(F) = 59 + 6.7\ P_3 - 2.3\ P_9 \pm 18$ $\quad R = 0.78$

Diplopoda (millipedes)

Total

$A_y = 4642 - 0.33\ T_4 - 233\ P_4 + 3.6\ P_5 + 58\ P_6 + 0.33\ PP \pm 315$ $\quad R = 0.80$

$A_m = -225 + 29\ P_6 + 0.31\ TP_2 \pm 104$ $\quad R = 0.65$

$A_y(B) = 20{,}737 - 594\ T_8 + 4.3\ T_{11} + 0.60\ PP \pm 58$ $\quad R = 0.92$

$A_m(B) = 5586 - 157\ T_8 + 1.1\ T_{11} - 5.2\ P_7 - 0.09\ TP_2 + 0.24\ PP \pm 17$ $\quad R = 0.94$

Scytonotus granulatus

$A_y = 28 + 0.43\ \mathrm{PP} \pm 71$ $R = 0.43$

$A_m = 12 + 0.22\ \mathrm{PP} \pm 32$ $R = 0.47$

$A_y(\mathrm{B}) = -12 + 3.7\ \mathrm{T}_{13} - 3.1\ \mathrm{P}_3 \pm 18$ $R = 0.77$

$A_m(\mathrm{F}) = -50 + 0.008\ \mathrm{T}_5 + 1.1\ \mathrm{P}_6 + 0.25\ \mathrm{PP} \pm 2.6$ $R = 0.84$

Cleidogona caesioannulata

$A_y = 19.5 + 0.52\ \mathrm{PP} \pm 55$ $R = 0.52$

Chilopoda (centipedes)

Total

$A_y = 87 + 0.73\ \mathrm{PP} \pm 173$ $R = 0.73$

$A_m = 72 - 17\ \mathrm{P}_2 + 1.3\ \mathrm{P}_{11} + 0.11\ \mathrm{PP} \pm 30$ $R = 0.78$

$A_y(\mathrm{F}) = -939 - 15\ \mathrm{P}_8 - 0.18\ \mathrm{TP}_3 + 9.1\ \mathrm{U}_1 + 0.60\ \mathrm{PP} \pm 50$ $R = 0.94$

$A_m(\mathrm{F}) = -2260 + 70\ \mathrm{T}_1 - 0.58\ \mathrm{T}_4 - 0.02\ \mathrm{T}_6 - 3.8\ \mathrm{P}_8 + 0.93\ \mathrm{S}_1 + 0.85\ \mathrm{U}_1 + 0.11\ \mathrm{PP} \pm 4.9$ $R = 0.99$

Geophilidae

$A_y = 25 + 0.82\ \mathrm{PP} \pm 92$ $R = 0.81$

$A_m = 12 + 0.17\ \mathrm{PP} \pm 21$ $R = 0.79$

$A_y(\mathrm{F}) = -945 - 11\ \mathrm{P}_8 + 10\ \mathrm{S}_1 - 0.35\ \mathrm{S}_2 + 7.7\ \mathrm{U}_1 + 0.78\ \mathrm{PP} \pm 32$ $R = 0.95$

$A_m(\mathrm{F}) = 249 - 1.6\ \mathrm{T}_9 - 2.0\ \mathrm{P}_4 - 2.2\ \mathrm{P}_8 - 0.62\ \mathrm{P}_9 + 0.04\ \mathrm{TP}_2 + 0.10\ \mathrm{PP} \pm 4.4$ $R = 0.98$

Orthoptera

Total

$A_y = -70 + 0.01\ \mathrm{T}_{10} + 0.02\ \mathrm{P}_5 + 0.58\ \mathrm{PP} \pm 10$ $R = 0.86$

$A_m = -3.2 + 0.96\ \mathrm{P}_7 + 0.21\ \mathrm{PP} \pm 5.5$ $R = 0.69$

$A_y(\mathrm{F}) = -89 - 3.2\ \mathrm{P}_2 + 1.5\ \mathrm{P}_4 - 0.13\ \mathrm{P}_{10} + 0.68\ \mathrm{U}_1 \pm 5.4$ $R = 0.91$

$A_m(\mathrm{F}) = -18 + 0.46\ \mathrm{P}_3 - 0.02\ \mathrm{P}_{11} + 0.18\ \mathrm{U}_1 \pm 1.6$ $R = 0.83$

Diapheromera femorata

$A_y = -5.8 + 0.002\ \mathrm{T}_{10} + 0.43\ \mathrm{PP} \pm 1.7$ $R = 0.64$

$A_m = -1.4 + 0.07\ \mathrm{P}_9 + 0.16\ \mathrm{PP} \pm 0.75$ $R = .67$

$A_y(\mathrm{B}) = 17 - 0.001\ \mathrm{T}_{12} - 0.05\ \mathrm{U}_2 + 0.43\ \mathrm{PP} \pm 0.73$ $R = 0.83$

Oecanthus angustipennis

$A_y = -11 + 1.0\ \mathrm{P}_6 + 0.03\ \mathrm{TP}_2 \pm 7.8$ $R = 0.53$

$A_y(\mathrm{BEP}) = 1539 - 43\ \mathrm{T}_8 + 0.30\ \mathrm{T}_{11} + 2.0\ \mathrm{P}_2 + 1.3\ \mathrm{P}_6 - 0.05\ \mathrm{TP}_3 \pm 6.8$ $R = 0.71$

$A_m = -2.2 + 0.02\ \mathrm{TP}_2 \pm 4.6$ $R = 0.46$

Hemiptera

Total

$A_y = -2210 + 0.16\ T_{12} + 7.1\ U_2 + 0.57\ PP \pm 122$ $R = 0.72$

$A_m = 39 + 2.2\ S_1 \pm 31$ $R = 0.54$

$A_m(F) = -1218 + 0.07\ T_{11} + 8.2\ T_{13} - 0.33\ P_{11} + 6.4\ U_1 \pm 24$ $R = 0.91$

Zelus exsanguis

$A_y = 9.4 - 1.4\ P_3 + 1.1\ P_6 + 0.35\ PP \pm 8.0$ $R = 0.60$

$A_y(BEP) = 4313 - 84\ T_2 + 0.59\ T_5 - 36\ T_7 + 0.28\ T_{10} - 1.4\ P_3 - 5.6\ P_4 + 0.08\ P_5 - 0.025\ TP_3 \pm 5.8$ $R = 0.85$

$A_m = 61 - 0.47\ T_7 - 0.72\ P_3 + 0.76\ P_6 - 0.03\ P_{11} - 0.20\ U_1 \pm 3.3$ $R = 0.74$

$A_m(BEP) = 1944 - 36\ T_2 + 0.25\ T_5 - 20\ T_7 + 0.16\ T_{10} - 0.37\ P_3 + 0.04\ P_{10} \pm 2.8$ $R = 0.82$

Nabis spp., total

$A_y = -75 + 0.08\ TP_1 + 0.12\ TP_3 + 0.18\ S_1 + 0.75\ PP \pm 17$ $R = 0.92$

nymphs only

$A_m = -37 + 0.007\ T_{10} + 0.01\ P_5 \pm 6.3$ $R = 0.66$

$A_y(F) = 5.2 + 0.58\ PP \pm 8.1$ $R = 0.59$

$A_m(F) = 2.4 + 0.26\ PP \pm 2.8$ $R = 0.68$

Gargaphia tiliae

$A_y = -55 + 4.1\ T_{13} + 0.58\ PP \pm 42$ $R = 0.65$

$A_m = 5.7 + 0.26\ PP \pm 20$ $R = 0.58$

$A_y(B) = 12{,}744 - 341\ T_3 + 2.3\ T_6 \pm 12$ $R = 0.81$

$A_m(B) = 10{,}369 - 277\ T_3 + 1.9\ T_6 \pm 11$ $R = 0.77$

Corythuca aesculi

$A_y = -325 + 1.7\ U_2 + 0.52\ PP \pm 40$ $R = 0.64$

$A_y(BEP) = 3088 - 144\ T_1 + 1.1\ T_4 - 0.05\ T_6 - 242\ T_7 + 264\ T_8 + 1.9\ T_{10} - 1.8\ T_{11} - 5.1\ P_6 - 4.0\ P_8 - 0.17\ TP_2 \pm 29$ $R = 0.88$

$A_m = -142 + 0.75\ U_2 + 0.22\ PP \pm 15$ $R = 0.67$

$A_m(BEP) = 13{,}809 + 269\ T_3 - 1.8\ T_6 - 146\ T_7 + 212\ T_9 + 1.2\ T_{10} - 0.05\ T_{11} - 1.4\ T_{12} - 2.6\ T_{13} + 91\ P_2 - 7.4\ P_3 + 18\ P_4 - 0.19\ P_5 - 3.6\ P_7 - 8.6\ P_8 - 0.44\ P_{10} - 2.4\ P_{11} + 0.12\ TP_1 - 0.90\ TP_2 - 0.67\ TP_3 - 5.5\ S_1 + 0.10\ S_2 + 1.2\ U_1 - 1.8\ U_2 + 0.17\ PP \pm 6.5$ $R = 0.98$

Lygus lineolaris

$A_y = 5.2 + 0.06\ TP_1 + 0.45\ PP \pm 20$ $R = 0.74$

$A_y(BEP) = 7875 - 149\ T_2 + 1.04\ T_5 - 82\ T_7 + 0.65\ T_{10} + 0.16\ P_{10} + 0.38\ PP \pm 19$ $R = 0.80$

$A_m = 11 - 1.5\ P_3 + 0.10\ P_{10} + 0.34\ PP \pm 10$ $R = 84$

$A_m(\mathrm{BEP}) = 5275 - 95\ T_2 + 65\ T_5 - 72\ T_7 + 0.58\ T_{10} + 0.02\ T_{11} + 2.3\ T_{13} - 16\ P_1 - 107\ P_2 + 2.8\ P_3 - 1.5\ P_4 - 2.4\ P_6 + 5.3\ P_8 + 1.1\ P_{10} + 2.7\ P_{11} + 0.07\ TP_1 + 1.0\ TP_2 + 0.86\ TP_3 + 6.6\ S_1 - 0.13\ S_2 + 2.2\ U_2 + 0.36\ PP \pm 5.0$ $R = 0.98$

Horcias dislocatus

$A_y = -8.1 + 0.002\ T_4 + 0.39\ PP \pm 2.8$ $R = 0.48$

$A_m = -53 - 0.01\ T_4 + 0.02\ T_5 + 0.08\ TP_3 \pm 17$ $R = 0.66$

$A_y(\mathrm{B}) = -2.5 + 0.61\ P_8 \pm 2.8$ $R = 0.59$

Dicyphus gracilentus

$A_y = -227 - 4.7\ P_6 + 0.06\ S_2 + 2.2\ U_1 \pm 31$ $R = 0.67$

$A_y(\mathrm{BEP}) = 17{,}234 - 340\ T_2 + 2.4\ T_5 - 170\ T_7 + 1.3\ T_{10} - 52\ P_1 - 65\ P_2 + 0.06\ P_5 - 7.7\ P_6 + 9.9\ P_8 - 3.6\ P_9 + 2.9\ P_{10} + 3.3\ P_{11} - 0.16\ TP_1 + 0.24\ TP_2 + 2.4\ S_1 + 2.4\ U_1 + 2.1\ U_2 + 0.33\ PP \pm 18$ $R = 0.95$

$A_m = 126 - 3.5\ P_6 + 0.04\ S_2 + 1.2\ U_1 \pm 21$ $R = 0.67$

$A_m(\mathrm{BEP}) = 7407 - 207\ T_2 + 1.4\ T_5 - 36\ P_1 - 138\ P_2 + 0.04\ P_5 + 8.5\ P_8 - 4.0\ P_9 + 1.9\ P_{10} + 2.9\ P_{11} - 0.09\ TP_1 + 1.4\ TP_2 + 1.1\ TP_3 + 2.8\ S_1 + 2.6\ U_2 + 0.27\ PP \pm 16$ $R = 0.90$

Blissus leucopterus

$A_y = 14{,}503 - 413\ T_8 + 2.9\ T_{11} + 0.47\ PP \pm 45$ $R = 0.92$

$A_m = 6177 - 176\ T_8 + 1.2\ T_{11} + 0.14\ PP \pm 26$ $R = 0.82$

Jalysus spinosus

$A_y = 66 - 0.80\ T_9 \pm 3.6$ $R = 0.50$

$A_y(\mathrm{BEP}) = -28 + 0.52\ P_7 + 0.23\ U_1 \pm 3.5$ $R = 0.54$

$A_m = 11.8 - 0.002\ T_{12} \pm 1.6$ $R = 0.37$

$A_m(\mathrm{BEP}) = -0.10 + 0.19\ P_7 + 0.09\ U_1 \pm 1.5$ $R = 0.48$

$A_y(\mathrm{F}) = -88 + 0.95\ P_1 + 0.43\ U_2 \pm 3.4$ $R = 0.79$

$A_m(\mathrm{F}) = -36 + 0.03\ P_{10} + 0.12\ U_1 + 0.11\ U_2 \pm 1.3$ $R = 0.82$

HOMOPTERA (leafhoppers, others)

Total

$A_y(\mathrm{F}) = 361 - 0.62\ TP_2 + 0.65\ PP \pm 154$ $R = 0.78$

$A_m = -65 + 16\ P_7 + 0.17\ PP \pm 81$ $R = 0.57$

Osbornellus auronitens

$A_y = 1.6 + 0.60\ PP \pm 3.0$ $R = 0.60$

$A_m(\mathrm{BEP}) = 406 - 11.8\ T_8 + 0.08\ T_{11} + 0.32\ P_6 + 0.12\ U_1 + 0.32\ PP \pm 1.9$ $R = 0.69$

$A_m = -1.9 + 0.002\ P_5 + 0.36\ PP \pm 2.0$ $R = 0.57$

$A_m(\mathrm{B}) = -16 - 0.004\ TP_3 + 0.14\ U_1 + 0.31\ PP \pm 0.95$ $R = 0.79$

DIPTERA (flies)

Total

$A_y = -993 + 1.4\ P_5 - 8.7\ P_{10} + 0.69\ PP \pm 570$ $R = 0.85$

$A_m = -417 + 13\ P_4 + 0.18\ PP \pm 145$ $R = 0.81$

larvae, excluding Tipulidae

$A_y = -1586 + 46\ P_4 + 0.83\ PP \pm 460$ $R = 0.86$

$A_m = 36 + 0.21\ PP \pm 119$ $R = 0.84$

$A_y(F) = -1804 + 28\ T_{13} - 35\ P_9 + 14\ U_2 + 0.57\ PP \pm 118$ $R = 0.94$

$A_m(F) = -715 + 0.06\ T_4 + 34\ T_{13} + 4.3\ P_2 - 78\ P_6 + 14\ P_9 - 0.84\ P_{10} + 0.17\ TP_3 + 1.0\ U_2 + 0.12\ PP \pm 7.7$ $R = 0.999$

Tipulidae (adults)

$A_y = -26 + 0.02\ P_5 + 1.4\ P_7 + 0.52\ PP \pm 10$ $R = 0.74$

$A_y(BEP) = 3700 - 108\ T_2 + 0.76\ T_5 - 1.1\ T_{13} + 0.02\ P_5 + 3.0\ S_1 - 0.09\ S_2 + 0.74\ U_2 + 0.48\ PP \pm 8.9$ $R = 0.85$

$A_m = -9.1 + 0.35\ P_4 + 0.15\ PP \pm 4.8$ $R = 0.51$

$A_m(B) = -47 - 0.007\ T_5 + 0.80\ T_{13} + 0.79\ P_1 + 0.53\ U_1 + 0.22\ PP \pm 3.2$ $R = 0.91$

larvae

$A_y = -31 + 7.2\ P_6 + 0.42\ PP \pm 53$ $R = 0.54$

$A_m = 12 + 0.17\ PP \pm 24$ $R = 0.41$

$A_m(F) = 7.9 - 0.79\ T_2 + 0.68\ T_7 + 0.62\ T_{13} \pm 3.2$ $R = 0.80$

Sympycnus lineatus (adults)

$A_y = -5.9 + 0.02\ P_5 \pm 19$ $R = 0.45$

$A_m = 4.8 + 0.10\ P_{11} \pm 9.9$ $R = 0.46$

$A_y(B) = -66 + 0.76\ T_1 - 7.0\ T_3 - 0.02\ T_5 + 4.5\ T_7 + 3.0\ T_8 + 2.7\ T_{13} + 26\ P_1 - 1.4\ P_{10} + 0.01\ S_2 + 0.23\ PP \pm 3.8$ $R = 0.99$

$A_m(F) = -5.2 + 1.7\ P_3 \pm 6.1$ $R = 0.67$

Pseudogriphoneura crevecoeuri (adults)

$A_y = 9178 - 244\ T_9 + 1.6\ T_{12} + 2.9\ P_6 + 0.32\ PP \pm 11$ $R = 0.85$

$A_m = 4830 - 129\ T_9 + 0.9\ T_{12} + 2.0\ P_6 + 0.22\ PP \pm 6.9$ $R = 0.83$

$A_m(BEP) = 3923 + 38\ T_1 - 0.31\ T_4 - 133\ T_9 + 0.89\ T_{12} + 7.5\ P_1 - 8.2\ P_4 + 0.11\ P_5 + 2.4\ P_6 - 0.35\ P_{10} - 1.6\ S_1 + 0.05\ S_2 + 0.16\ PP \pm 6.0$ $R = 0.91$

Thaumatomyia glabra (adults)

$A_y = 3.0 - 0.006\ TP_1 + 0.36\ PP \pm 2.1$ $R = 0.49$

$A_m = 2.3 - 0.10\ P_8 - 0.003\ TP_1 + 0.17\ PP \pm 0.75$ $R = 0.66$

$A_m(\text{F}) = -0.33 - 0.23\ \text{P}_1 + 0.003\ \text{P}_5 - 0.003\ \text{TP}_1 \pm 0.49$ $\quad R = 0.83$

Drosophila quinaria (*adults*)

No significant regressions.

LEPIDOPTERA (moths, butterflies)

Total

$A_y = -39 + 17\ \text{T}_{13} - 26\ \text{P}_6 + 15\ \text{P}_7 \pm 80$ $\quad R = 0.81$

larvae

$A_y = 34 + 16\ \text{T}_{13} - 21\ \text{P}_6 \pm 75$ $\quad R = 0.79$

$A_m = 65 - 1.6\ \text{S}_1 \pm 29$ $\quad R = 0.44$

$A_y(\text{B}) = -139 + 0.06\ \text{T}_{11} + 12\ \text{T}_{13} - 5.0\ \text{P}_4 - 11\ \text{P}_6 \pm 43$ $\quad R = 0.91$

$A_m(\text{B}) = -110 + 1.7\ \text{T}_7 + 4.3\ \text{T}_{13} - 1.3\ \text{P}_9 + 0.02\ \text{S}_2 \pm 9.3$ $\quad R = 0.92$

Dichomeris ligulella (*adults*)

$A_y = -4.6 + 0.60\ \text{T}_{13} \pm 7.6$ $\quad R = 0.33$

$A_m(\text{BEP}) = 2642 - 63\ \text{T}_2 + 117\ \text{T}_3 + 0.42\ \text{T}_5 - 0.76\ \text{T}_6 - 27\ \text{T}_7 - 3.2\ \text{T}_8 + 45\ \text{T}_9 + 0.22\ \text{T}_{10} - 0.28\ \text{T}_{12} + 0.64\ \text{T}_{13} - 8.8\ \text{P}_1 - 49\ \text{P}_2 - 1.2\ \text{P}_3 - 9.3\ \text{P}_4 + 0.15\ \text{P}_5 - 0.81\ \text{P}_6 - 3.7\ \text{P}_7 + 0.40\ \text{P}_{10} + 1.0\ \text{P}_{11} + 0.46\ \text{TP}_2 + 0.42\ \text{TP}_3 + 0.01\ \text{S}_2 - 0.27\ \text{U}_1 + 0.86\ \text{U}_2 + 0.51\ \text{PP} \pm 2.6$ $\quad R = 0.97$

$A_y(\text{F}) = -3.2 + 0.32\ \text{T}_{13} \pm 1.8$ $\quad R = 0.51$

COLEOPTERA (beetles — adults except where indicated)

Total (*adults, larvae*)

$A_y = -10{,}451 + 146\ \text{T}_7 + 72\ \text{T}_{13} + 2.0\ \text{P}_5 \pm 719$ $\quad R = 0.79$

$A_m = -4141 + 54\ \text{T}_7 + 26\ \text{P}_4 + 0.98\ \text{TP}_3 \pm 268$ $\quad R = 0.74$

$A_m(\text{F}) = -3524 + 0.56\ \text{T}_{10} + 57\ \text{P}_4 - 0.93\ \text{TP}_2 \pm 228$ $\quad R = 0.85$

larvae, excluding Ptilodactyla

$A_y = 77 + 0.70\ \text{PP} \pm 296$ $\quad R = 0.73$

$A_m = 34 + 0.15\ \text{PP} \pm 102$ $\quad R = 0.55$

$A_y(\text{B}) = -5972 + 0.11\ \text{T}_6 + 14\ \text{T}_8 + 56\ \text{T}_9 + 30\ \text{P}_7 + 3.9\ \text{P}_{11} - 0.68\ \text{TP}_3 + 0.21\ \text{PP} \pm 66$ $\quad R = 0.96$

$A_m(\text{B}) = 9009 + 0.02\text{T}_6 + 4.1\ \text{T}_8 - 267\ \text{T}_9 + 1.9\ \text{T}_{12} + 11\ \text{P}_7 + 1.3\ \text{P}_{11} - 0.22\ \text{TP}_3 \pm 15$ $\quad R = 0.98$

Carabidae

$A_y = 1130 - 17\ \text{P}_6 - 7.0\ \text{U}_1 \pm 80$ $\quad R = 0.61$

$A_y(\text{F}) = -1090 + 12\ \text{T}_{13} + 9.0\ \text{P}_7 + 0.38\ \text{P}_{10} - 0.17\ \text{P}_{11} + 6.6\ \text{U}_1 + 0.34\ \text{PP} \pm 17$ $\quad R = 0.98$

$A_m(\text{F}) = -438 + 4.5\ \text{T}_{13} + 2.2\ \text{P}_1 + 2.9\ \text{P}_7 + 2.7\ \text{U}_1 \pm 8.2$ $\quad R = 0.94$

Staphylinidae spp.

$A_y = -80{,}333 + 0.57\ T_4 + 2396\ T_7 - 19\ T_{10} + 106\ P_7 - 6.6 P_{11} + 5.0\ TP_1 \pm 367$ $R = 0.92$

$A_m = -497 + 64\ P_7 - 2.6\ P_{11} + 1.8\ TP_1 \pm 230$ $R = 0.80$

$A_m(F) = 587 - 14\ T_9 + 0.15\ T_{10} \pm 56$ $R = 0.84$

Notoxus spp.

$A_y = -704 + 0.13\ T_{12} + 0.35\ PP \pm 96$ $R = 0.60$

$A_m = 10{,}623 - 336\ T_1 + 2.7\ T_4 + 0.08\ T_{12} - 6.9\ P_6 - 2.8\ U_1 + 0.19\ PP \pm 49$ $R = 0.81$

$A_y(F) = -\ 10 + 0.17\ S_2 + 0.44\ PP \pm 65$ $R = 0.80$

$A_m(B) = 2707 - 86\ T_1 + 0.70\ T_4 - 6.6\ P_6 - 0.11\ TP_1 \pm 16.5$ $R = 0.82$

Ptilodactyla serricollis (adults)

$A_y = -12 + 2.0\ P_7 \pm 9.6$ $R = 0.52$

$A_y(BEP) = 4318 + 33\ T_7 - 49\ T_8 - 93\ T_9 - 0.27\ T_{10} + 0.34\ T_{11} + 0.6\ T_{12} + 1.3\ P_6 + 1.6\ P_7 \pm 8.0$ $R = 0.75$

$A_m = -7.8 + 1.4\ P_7 \pm 6.6$ $R = 0.51$

$A_y(B) = 28 - 6.7\ P_2 + 0.53\ P_{11} - 0.03\ TP_1 - 0.01\ TP_3 \pm 3.3$ $R = 0.92$

$A_m(B) = 41 - 3.9\ P_2 + 0.29\ P_{11} - 0.01 TP_1 - 0.13\ U_2 \pm 1.8$ $R = 0.93$

larvae

$A_y = -324 + 3.0\ T_{12} + 8.4\ T_{13} + 0.09\ P_5 + 6.7\ S_1 + 0.39\ PP \pm 71$ $R = 0.73$

$A_m = -142 + 4.1\ T_{13} + 0.04\ P_5 + 3.3\ S_1 \pm 41$ $R = 0.59$

$A_m(BEP) = -1322 + 5.4\ T_9 + 46\ P_2 - 6.7\ P_3 + 34\ P_4 - 0.39\ P_5 + 6.9\ P_6 - 12\ P_8 + 5.4\ P_9 - 3.2\ P_{11} \pm 31$ $R = 0.85$

$A_y(B) = 338 + 5.6\ T_7 - 3.1\ T_{13} - 6.6\ P_3 + 0.14\ P_5 - 4.1\ P_8 - 0.14\ TP_1 - 5.1\ U_1 \pm 20$ $R = 0.95$

$A_m(B) = 173 + 2.7\ T_7 - 1.5\ T_{13} - 4.6\ P_3 + 0.08\ P_5 - 0.79\ P_9 - 0.07\ TP_1 - 2.4\ U_1 \pm 8.8$ $R = 0.96$

Telephanus velox

$A_y = 35{,}659 - 1051\ T_7 - 40\ T_9 + 8.6\ T_{10} - 17\ P_4 + 0.35\ TP_3 \pm 161$ $R = 0.80$

$A_m = 35{,}022 - 1057\ T_7 - 30\ T_9 + 8.7\ T_{10} - 14\ P_4 \pm 160$ $R = 0.75$

Melanophthalma spp.

$A_y = 8.0 + 0.58\ TP_3 \pm 164$ $R = 0.50$

$A_y(BEP) = -23 + 11\ P_6 + 0.56\ PP \pm 70$ $R = 0.62$

$A_m = -59 + 0.43\ TP_3 \pm 117$ $R = 0.52$

$A_m(BEP) = -9.0 + 4.0\ P_6 + 0.14\ PP \pm 20$ $R = 0.62$

$A_y(B) = -1195 - 21\ P_1 + 12\ U_1 \pm 72$ $R = 0.78$

$A_m(B) = -510 + 0.04\ T_{10} + 0.14\ TP_3 + 2.9\ U_1 \pm 33$ $R = 0.76$

Diabrotica undecimpunctata howardi

$A_y = 8.3 - 0.66\ P_6 \pm 3.7$ $R = 0.44$

$A_y(\text{BEP}) = 1694 - 16\ T_1 - 19\ T_2 + 0.13\ T_4 + 0.13\ T_5 - 16\ T_7 + 0.13\ T_{10} - 0.88\ P_6 \pm 2.7$ $R = 0.81$

$A_m = 2.6 - 0.48\ P_6 + 0.30\ P_8 + 0.22\ \text{PP} \pm 2.5$ $R = 0.63$

$A_m(\text{BEP}) = 443 - 13\ T_1 + 0.11\ T_4 - 0.52\ P_6 + 0.29\ P_8 - 0.12\ U_1 \pm 2.0$ $R = 0.75$

$A_m(\text{F}) = -16 + 0.004\ T_{12} - 0.39\ P_2 - 0.22\ P_3 + 0.01\ \text{TP}_1 \pm 0.75$ $R = 0.94$

Acalymma vittata

$A_y = 10 + 0.98\ P_3 - 1.0\ P_8 + 0.27\ \text{PP} \pm 8.9$ $R = 0.67$

$A_m = -1.9 + 1.0\ P_3 \pm 6.9$ $R = 0.43$

$A_y(\text{B}) = -115 + 0.009\ T_6 + 0.67\ T_{13} + 0.48\ U_1 \pm 3.1$ $R = 0.86$

$A_m(\text{B}) = -49 + 0.004\ T_6 + 0.003\ T_{11} + 0.14\ U_1 \pm 1.9$ $R = 0.76$

Cerotoma trifurcata

$A_y = -598 + 0.11\ T_{12} + 0.56\ \text{PP} \pm 48$ $R = 0.83$

$A_m = -365 + 5.0\ T_9 + 0.16\ \text{PP} \pm 13$ $R = 0.84$

$A_m(\text{F}) = 114 + 2.5\ T_3 - 19\ P_4 + 0.23\ P_5 - 1.4\ P_9 + 1.1\ U_1 + 0.19\ \text{PP} \pm 6.0$ $R = 0.98$

Baliosus ruber

$A_y = 32 + 0.004\ T_5 - 0.38\ U_1 + 0.24\ \text{PP} \pm 4.5$ $R = 0.66$

$A_m = 23 - 0.17\ U_1 + 0.09\ \text{PP} \pm 2.1$ $R = 0.61$

$A_y(\text{F}) = -1.8 + 0.16\ T_{13} \pm 0.55$ $R = 0.69$

$A_m(\text{B}) = 8.8 - 0.008\ P_{10} - 0.04\ U_2 \pm 0.44$ $R = 0.72$

Sumitrosis spp.

No significant regressions.

Apion spp.

$A_y = -18 + 0.004\ T_{12} \pm 3.4$ $R = 0.39$

$A_m = 2.4 - 0.002\ S_2 \pm 1.9$ $R = 0.35$

$A_y(\text{B}) = -22 + 0.003\ T_{11} + 0.21\ P_9 + 0.01\ P_{11} + 0.51\ \text{PP} \pm 1.2$ $R = 0.82$

$A_m(\text{B}) = -11 + 0.12\ T_1 - 0.12\ P_8 + 0.16\ P_9 + 0.004\ \text{TP}_2 - 0.09\ S_1 \pm 0.69$ $R = 0.88$

Idiostethus spp.

$A_y = 723 - 4.2\ T_3 - 0.02\ T_4 - 3.3\ T_7 + 2.4\ P_3 - 1.0\ U_1 \pm 13$ $R = 0.81$

$A_m = 1615 - 2.6\ T_3 - 40\ T_7 + 0.31\ T_{10} - 0.69\ U_1 \pm 8.9$ $R = 0.76$

$A_m(\text{BEP}) = 12{,}243 - 1.2\ T_1 - 89\ T_2 - 217\ T_3 + 0.57\ T_5 + 1.3\ T_6 - 17\ P_1 - 174\ P_2 + 2.8\ P_3 + 2.0\ P_6 + 2.9\ P_8 - 0.83\ P_9 + 0.95\ P_{10} + 1.1\ P_{11} + 2.2\ \text{TP}_2 + 2.0\ \text{TP}_3 - 2.9\ S_1 + 0.09\ S_2 - 0.99\ U_1 + 1.2\ U_2 \pm 6.5$ $R = 0.94$

Lechriops oculatus

$A_y = -30 + 0.53\ T_1 + 0.50\ PP \pm 4.8$ $R = 0.61$
$A_m = 1.8 + 0.14\ PP \pm 2.1$ $R = 0.37$
$A_y(F) = -32 + 0.25\ U_1 \pm 1.9$ $R = 0.65$
$A_m(B) = -16 + 0.23\ T_3 - 0.14\ P_8 \pm 0.95$ $R = 0.65$

FORMICIDAE (ants)

Total, ground

$A_y = -117 + 0.65\ P_5 \pm 431$ $R = 0.50$
$A_m = 45 + 29\ P_3 \pm 207$ $R = 0.39$
$A_y(B) = 364 + 0.21 T_{10} - 46\ P_3 - 35\ P_8 - 0.62\ TP_1 + 0.32\ PP \pm 128$ $R = 0.92$
$A_m(F) = -2492 - 18\ T_1 + 0.77\ T_6 - 20\ T_{13} - 384\ P_1 + 21\ P_9 + 25\ P_{10} + 2.3\ P_{11} + 0.44\ PP \pm 20$ $R = 0.999$

herbs and shrubs

$A_y = -21 + 0.05\ P_5 + 0.48\ PP \pm 39$ $R = 0.61$
$A_m = -15 + 0.02\ P_5 + 0.19\ PP \pm 17$ $R = 0.60$
$A_m(BEP) = -671 + 0.03\ T_6 + 0.02\ T_{12} + 1.9\ P_9 + 0.09\ TP_2 + 1.4\ U_2 \pm 17$ $R = 0.65$

Aphaenogaster rudis

$A_y = 12 + 0.79\ P_{11} \pm 84$ $R = 0.40$
$A_m = 113 - 9.0\ T_2 + 8.0\ T_8 \pm 61$ $R = 0.49$
$A_m(F) = -632 + 8.4\ T_7 + 11\ T_{13} \pm 48$ $R = 0.72$

Ponera pennsylvanica

$A_y = 1280 - 18\ T_7 + 0.37\ PP \pm 155$ $R = 0.56$
$A_m = 477 - 6.9\ T_7 + 0.20\ PP \pm 58$ $R = 0.64$
$A_y(F) = -205 + 0.16\ T_{10} - 29\ P_8 \pm 104$ $R = 0.74$

GASTROPODA (snails, slugs)

Total

$A_y(B) = -936 + 8.2\ U_1 \pm 83$ $R = 0.54$
$A_m(B) = 16 + 1.2\ S_1 \pm 18$ $R = 0.52$
$A_y(F) = -1588 + 13\ U_1 + 0.63\ PP \pm 109$ $R = 0.82$
$A_m(F) = -345 + 2.8\ U_1 + 0.11\ PP \pm 28$ $R = 0.73$

Carychium exile

No significant regressions.

Mesodon spp.

$A_y = -35 + 3.7\ T_{13} \pm 36$ $R = 0.42$
$A_y(BEP) = 11{,}427 - 302\ T_9 + 2.0\ T_{12} - 67\ P_2 + 1.0\ TP_2 + 0.90\ TP_3 + 0.34\ PP \pm 29$ $R = 0.73$
$A_m = -14 + 1.6\ T_{13} \pm 14$ $R = 0.44$
$A_m(BEP) = 3683 - 101\ T_2 + 0.70\ T_5 - 39\ P_2 + 0.59\ TP_2 + 0.54\ TP_3 \pm 13$ $R = 0.66$

$A_y(\mathrm{B}) = 126 + 1.5\ \mathrm{T}_2 + 2.5\ \mathrm{T}_{13} + 2.2\ \mathrm{P}_7 + 0.03\ \mathrm{S}_2 - 1.5\ \mathrm{U}_2 \pm 9.0$ $R = 0.88$

Retinella indentata

$A_y = 570 - 14\ \mathrm{T}_3 - 10\ \mathrm{P}_8 + 5.3\ \mathrm{U}_1 \pm 88$ $R = 0.59$

$A_m = -194 + 1.7\ \mathrm{U}_1 \pm 24$ $R = 0.43$

$A_y(\mathrm{F}) = -723 + 5.7\ \mathrm{U}_1 + 0.65\ \mathrm{PP} \pm 53$ $R = 0.82$

$A_m(\mathrm{B}) = -126 - 1.2\ \mathrm{P}_3 + 0.75\ \mathrm{U}_2 \pm 5.9$ $R = 0.80$

Hawaiia, Striatura, Punctum spp.

$A_y(\mathrm{F}) = -281 + 0.98\ \mathrm{S}_1 + 2.1\ \mathrm{U}_1 \pm 13$ $R = 0.85$

$A_m(\mathrm{F}) = -107 + 0.01\ \mathrm{S}_2 + 0.84\ \mathrm{U}_1 \pm 5.6$ $R = 0.84$

Haplotrema concavum

$A_y = -36 + 3.3\ \mathrm{T}_{13} + 0.38\ \mathrm{PP} \pm 28$ $R = 0.62$

$A_m = -12 + 1.4\ \mathrm{T}_{13} \pm 12$ $R = 0.47$

$A_y(\mathrm{B}) = -12 + 1.0\ \mathrm{T}_{13} + 0.32\ \mathrm{PP} \pm 5.1$ $R = 0.80$

$A_m(\mathrm{B}) = -42 + 0.61\ \mathrm{T}_8 + 0.34\ \mathrm{PP} \pm 3.9$ $R = 0.74$

Vertigo, Columella spp.

$A_y = 78 - 7.3\ \mathrm{P}_7 + 0.44\ \mathrm{PP} \pm 36$ $R = 0.58$

$A_m = 47 - 3.8\ \mathrm{P}_7 \pm 26$ $R = 0.38$

$A_m(\mathrm{F}) = 2.3 + 0.27\ \mathrm{PP} \pm 3.5$ $R = 0.57$

Succinea avara

$A_y = 12 + 0.55\ \mathrm{PP} \pm 61$ $R = 0.55$

$A_y(\mathrm{B}) = 14 + 0.65\ \mathrm{T}_{13} - 8.3\ \mathrm{P}_2 + 0.54\ \mathrm{P}_{11} + 0.02\ \mathrm{S}_2 \pm 4.0$ $R = 0.87$

$A_m(\mathrm{B}) = 29 - 0.47\ \mathrm{T}_7 - 3.0\ \mathrm{P}_2 + 0.63\ \mathrm{P}_6 + 0.65\ \mathrm{P}_7 + 0.22\ \mathrm{P}_{11} + 0.008\ \mathrm{S}_2 \pm 2.7$ $R = 0.93$

Deroceras spp.

$A_m(\mathrm{BEP}) = 1.8 - 1.7\ \mathrm{P}_7 + 1.0\ \mathrm{P}_9 - 2.7\ \mathrm{S}_1 + 0.07\ \mathrm{S}_2 \pm 11$ $R = 0.51$

$A_y(\mathrm{B}) = -189 + 0.04\ \mathrm{TP}_2 + 1.4\ \mathrm{U}_1 \pm 12$ $R = 0.70$

$A_m(\mathrm{B}) = -45 + 0.01\ \mathrm{TP}_2 + 0.35\ \mathrm{U}_1 \pm 3.8$ $R = 0.63$

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